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Evaluating the Role of Invasive Dreissenid Mussels on Harmful Algal Bloom Formation and Toxicity Using Citizen Science Data

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EVALUATING THE ROLE OF INVASIVE DREISSENID MUSSELS ON HARMFUL ALGAL BLOOM FORMATION AND TOXICITY USING CITIZEN SCIENCE DATA

by

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Abstract

V.G. Field. Evaluating the Role of Invasive Dreissenid Mussels on Harmful Algal Bloom Formation and Toxicity Using Citizen Science Data, 144 pages, 13 tables, 13 figures, 2020. APA style guide used.

Invasive dreissenid mussels cause ecological and economical damage to non-native freshwaters. Dreissenids are implicated as causative factors in cyanobacterial harmful algal bloom (HABs) formation and toxicity in low-nutrient lakes. I used data from the Citizen Statewide Lake Assessment Program (CSLAP) to assess variations in water quality and HAB parameters between invaded and uninvaded lakes in New York State. Only true color differed significantly between lake types, while HAB frequency did not. Instead, lake characteristics, water temperature, and nutrient status were drivers of HABs parameters. Open water microcystin concentrations were also a function of total nitrogen to total phosphorus ratios and did not differ based on invasion status. To better understand methods for monitoring dreissenid populations, an artificial substrate methodology was tested. The methodology did not provide sufficient information on either detection or population dynamics. Citizen science remains an imperative tool for understanding water quality, invasive species, and HABs.

Keywords: zebra mussel, quagga mussel, harmful algal blooms, microcystin, oligotrophic, mesotrophic, Great Lakes, limnology, artificial substrates, citizen science

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Chapter 1: Introduction

1.1 Harmful Algal Blooms (HABs)

1.1.1 Description of cyanobacterial HABs

Harmful algal blooms (HABs) in freshwater ecosystems are characterized as an excess growth of toxic cyanobacteria or algae. Cyanobacteria (formerly referred to as blue-green algae) constitute a large and diverse group of photosynthetic prokaryotes (Stanier and Cohen-Bazire 1977). Some genera of cyanobacteria, such as *Microcystis*, can produce cyanotoxins (O'Neil et al. 2012). The hepatotoxin microcystin has been linked to human illnesses including, pet illness and death, and livestock death (Azevedo et al. 2002; Trevino-Garrison et al. 2015; Carmichael and Boyer 2016; Svirčev et al. 2017). In the United States, the first documented case of human illness associated with microcystin occurred in 1931 when thousands of people developed gastroenteritis as a result of contaminated drinking water (Tisdale 1931). The risk to humans of toxins produced by HABs has prompted beach closures and drinking water advisories (US EPA 2015). HABs are most often characterized by the physical presentation of pea-soup green color and surface scum (Paerl et al. 2001). The spatial distribution of HABs within a lake is influenced by wind strength and direction and HABs are usually detected near the shoreline where the mass of the bloom has been pushed by wind and currents (Figueiras et al. 2006; Wu et al. 2015).

1.1.2 Temporal trends in HABs

A review of the global distribution of the cyanobacteria *Microcystis aeruginosa* found that *Microcystis* blooms had been reported in over 100 countries (Harke et al. 2016), an increase from earlier reports that cited fewer than 30 countries reporting *Microcystis* blooms (Zurawell et al. 2005). In the United States in the mid 20th century, cyanobacterial blooms were prevalent in

freshwater systems due to increased eutrophication. By the 1970s, lake management practices as well as legislation such as the Clean Water Act (1972) and the Great Lakes Water Quality Agreement (1978) to reduce nutrient input to freshwater systems initially led to reduction of HABs through the late 20th century (De Pinto et al. 1986). This reduction proved to be temporary, as the U.S. has seen increases in HABs in not only eutrophic, but also oligotrophic systems in the past two decades (Brooks et al. 2017). The increase in HABs prevalence cannot be attributed to one or a few factors alone, but rather the interactive effects of factors like global climate change (Paerl and Huisman 2008; O'Neil et al. 2012) and food web modifications caused by anthropogenic interference (e.g., overfishing, invasive species) (Heisler et al. 2008; O'Neil et al. 2012). In the U.S., HABs in the Laurentian Great Lakes have garnered extensive coverage and awareness. Lake Erie, the shallowest and most eutrophic Great Lake has experienced multiple years of HABs dominated by *Microcystis* (Bolsenga and Herdendorf 1993). A large bloom of high toxin concentration in 2011 covered nearly the entire western basin (Michalak et al. 2013). After a bloom in 2014, microcystin was detected in the drinking water in Toledo, Ohio at levels that exceeded the World Health Organization's guidelines (Steffen et al. 2017). This led to a drinking water advisory for 400,000 residents for more than two days. This event brought national attention to the threats posed by HABs and has prompted research into the conditions that promote HAB formation (Steffen et al. 2017; Watson et al. 2016).

The negative effects of HABs include threats to public health, recreation, and the freshwater ecosystem. Toxins from HABs present a variety of risks for the public health sector including contaminated drinking water, direct contact via swimming, fishing, and boating. If exposure occurs, cyanotoxins may cause adverse human health effects including nausea, gastrointestinal discomfort, and dermal irritation, especially in children (Weirich and Miller

2014). Cyanotoxins produced during HABs are linked to livestock deaths and illness in dogs (Trevino-Garrison et al. 2015). Recreation is also adversely affected by HABs due to beach closures (New York State Department of Health 2020). Currently there are some rapid analysis methods for toxin concentration of HABs available, but efficacy is limited (Watson et al. 2017). Toxic versus non-toxic HABs cannot be distinguished visually, and toxin concentration can vary greatly (Watson et al. 2017). Therefore, state and local agencies will close public beaches during a bloom event to significantly reduce or eliminate risk (New York State Department of Environmental Conservation 2019). Furthermore, HABs can impact the aquatic ecosystem. The bacterial decomposition of cyanobacteria demands increased oxygen, which may reduce available oxygen concentrations and lead to periods of local anoxia which can result in fish kills (Anderson et al. 2002).

1.1.3 Factors associated with the formation of HABs

There are many factors associated with the formation of HABs (**Figure 1-1**). Several abiotic factors are among the most understood drivers of the formation HABs. Low winds reduce vertical mixing in the water column leading proliferation of surface scum. Some cyanobacteria, including *Microcystis* can migrate vertically by using intracellular gas vacuoles (reviewed in Harke et al. 2016). Buoyancy regulation allows cyanobacteria to float to surface water and outcompete other phytoplankton for light during the day and migrate to the nutrient-rich hypolimnion at night (Reynolds and Walsby 1975; Huisman and Hulot 2005; Paerl and Huisman 2008). Nutrient enrichment is also associated with formation of HABs. Phosphorus and nitrogen, most often measured as total phosphorus (TP) (Schindler 1977, Correll 1998) and total nitrogen (TN) (Gobler et al. 2016, Newell et al. 2019) are known drivers of HABs. Increased global temperatures and severe weather events exacerbated by anthropogenic climate change can

directly and indirectly contribute to HAB formation (Paerl and Huisman 2008; Huisman et al. 2018). The growth rates of some cyanobacteria are maximized at high temperatures (Reynolds 2006; Paerl and Huisman 2008); further, the growth rate of cyanobacteria can increase at a steeper rate than the growth rate of other phytoplankton (Thomas and Litchman 2016). Increased global temperatures lead to more stable and longer periods of stratification in the water column. Stratification presents a selective advantage for those genera of cyanobacteria that can regulate their buoyancy. Buoyant cyanobacteria can shade out other phytoplankton during the day, and access additional nutrients in the hypolimnion at night (Walsby et al. 1997). Severe weather events like short, intense storms cause soil erosion in the watershed, leading to increased nutrient loading (Moss et al. 2017). Nutrient concentrations are further increased because of longer residence times from prolonged droughts in the summer (Paerl and Huisman 2017)

Historically, HABs were seen predominantly in eutrophic systems. Those events were predictable given that increased nutrient loading led to increased phytoplankton abundance and productivity. However, HABs are now documented in several oligotrophic and mesotrophic systems (Carey et al. 2012, Raikow et al. 2004). HABs in low nutrient (TP < 20 μg/L) lakes are perplexing because low-nutrient lakes do not have the expected nutrient conditions necessary for HABs.

Biotic factors are also known to influence the formation of HABs. Dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis rostriformis*; zebra and quagga mussels, respectively) can influence HABs formation differently in low nutrient and high nutrient contexts. In eutrophic systems, the addition of dreissenids is effective for reducing overall productivity and microcystin concentrations (Reeders et al. 1989; Smith et al. 1998). Further, the effects of dreissenids on microcystin concentration are reduced with the addition of TP (Sarnelle

et al. 2012). In low nutrient lakes, invasive dreissenid mussels are implicated in the promotion of toxin producing HABs (Vanderploeg et al. 2001, 2013; Raikow et al. 2004; Knoll et al. 2008). In a study of 39 low-nutrient (<20 μg/L TP) lakes, Knoll et al. (2008) found that lakes invaded by *D. polymorpha* resulted in 3.3 times higher microcystin concentrations than their uninvaded counterparts. Sarnelle et al. (2010) found that microcystin concentrations were significantly different between invaded and uninvaded lakes with TP <10 μg/L, with invaded lakes having greater microcystin concentrations. Some proposed mechanisms of dreissenid promotion of HABs that will be discussed in this thesis include: selective filtration (i.e., rejecting toxin-producing cyanobacteria back into the water column) combined with overall phytoplankton and zooplankton reduction, redistribution of essential nutrients like P and N from the water column to the benthos, and increased water clarity.

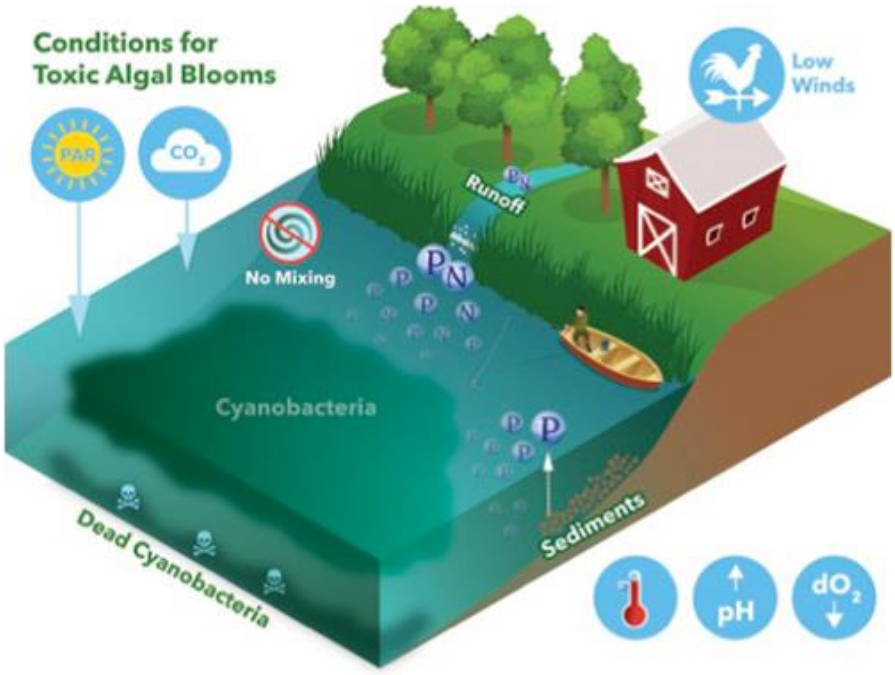


Figure 1-1. Causal factors of harmful algal bloom formation. (Image obtained from: https://www.ysi.com/ysi-blog/water-blogged-blog/2017/)

1.2 Dreissenids

1.2.1 Introduction to Great Lakes and inland lakes of New York

Dreissenid mussels are among the most prolific invasive aquatic species in North America. Native to the Ponto-Caspian region, dreissenid mussels are thought to have first been introduced to North America via ballast water emptied into Lake St. Clair by shipping vessels in the late 1980s (Mackie 1991). Since their introduction into the Great Lakes, dreissenids are found in freshwater systems all across New York State (Figure 1-2; Benson et al. 2013) and new invasions are still occurring due to anthropogenic activities like boating, recreation, and altered hydrology that connects bodies of water (Karatayev et al. 2015). Dreissenids are considered both non-native and invasive because they readily outcompete native mussels for habitat, food, and other resources (Schloesser and Masteller 1999; Strayer and Smith 1996). Dreissenids are called

116 “ecological engineers” (Figure 1-3; Coleman and Williams 2002) because they alter the physical,
117 biological, and chemical environment of the systems they invade. Shell litter from dead
118 dreissenids provides further habitat for new mussels to attach and might edge out native benthic
119 invertebrates (Ward and Ricciardi 2007). Filter feeding can reduce the abundance of
120 phytoplankton in the water column and lead to increased light penetration and water quality
121 (Higgins and Vander Zanden 2010). Increased water quality can be considered an ecosystem
122 service and is perceived as beneficial to business and homeowners (Limburg et al. 2009), but
123 dreissenids are still generally perceived as a nuisance invader. Filtering the water column can re-
124 distribute nutrients to the benthos. These effects are just a few examples of the ways in which
125 dreissenid mussels impact freshwater systems in North America.

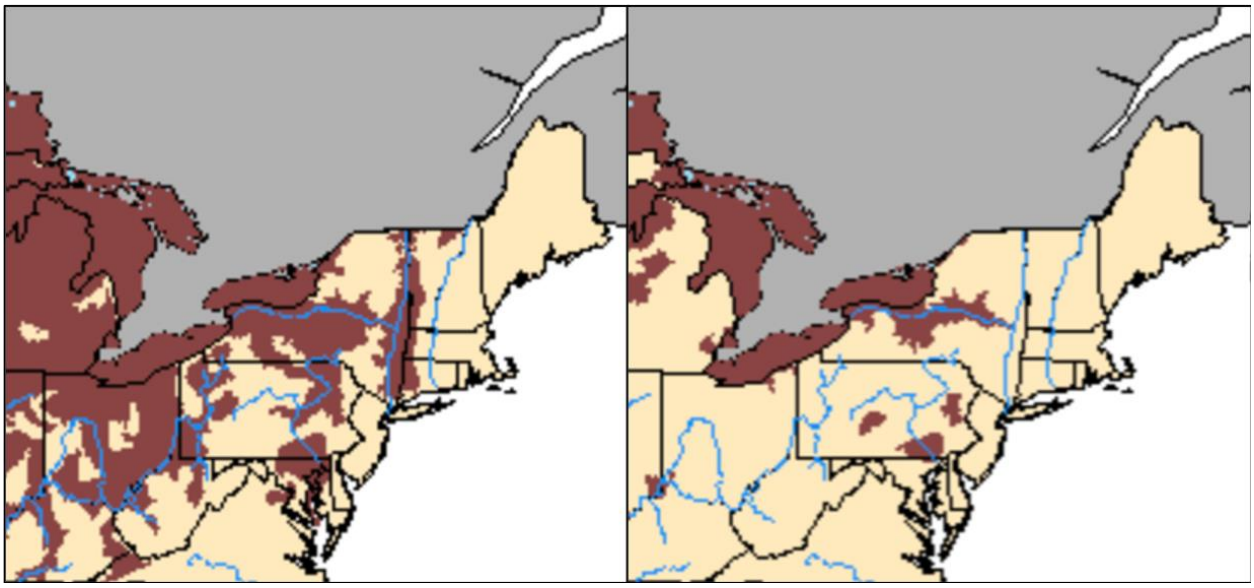


Figure 1-2. Geographic distribution of *Dreissena polymorpha* (left) and *Dreissena bugensis rostriformis* in the U.S. Northeast. Figure adapted from United States Geological Survey; updated February 2020. (Image obtained from: https://nas.er.usgs.gov/)

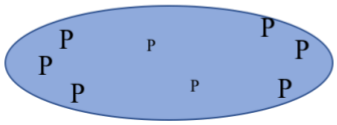
WATER CLARITY		High filtration rates (increased water clarity) Karatayev et al. (2015)
NUTRIENT STOICHIOMETRY	N:P	Change N:P ratio Arnott and Vanni (1996)
NUTRIENT DISTRIBUTION		External phosphorus input retained in the nearshore benthos ("Nearshore Phosphorus Shunt") Hecky et al. (2004)

Figure 1-3. Summary of the projected impacts of dreissenids as ecological engineers: how they can alter the physical, biochemical, and biological environment

1.2.2 Biological description

The biological characteristics of dreissenid mussels allow for quick and expansive invasion of freshwater systems. Its life cycle is represented by two distinct stages. The adult stage is a calciferous bivalve that attaches to surfaces via byssal threads, though further motility is possible should mussels seek better habitat (Nalepa and Schloesser 2013). The larval stage is a free-floating planktonic veliger, which allows for a quick spread of mussels between and throughout systems (Nalepa and Schloesser 2013). Dreissenid reproduction is primarily regulated by water temperature. Temperatures between 16 °C and 26 °C are optimal for the growth and reproduction of zebra mussels (Nalepa and Schloesser 2013). Dreissenids are obligate filter feeders. Markedly high filtration rates can cause drastic reductions in phytoplankton biomass in the water column (Figure 1-4; Nalepa et al. 1999; Noonburg et al. 2003). This is a characteristic that is an important part of the mechanism in the promotion of HABs.

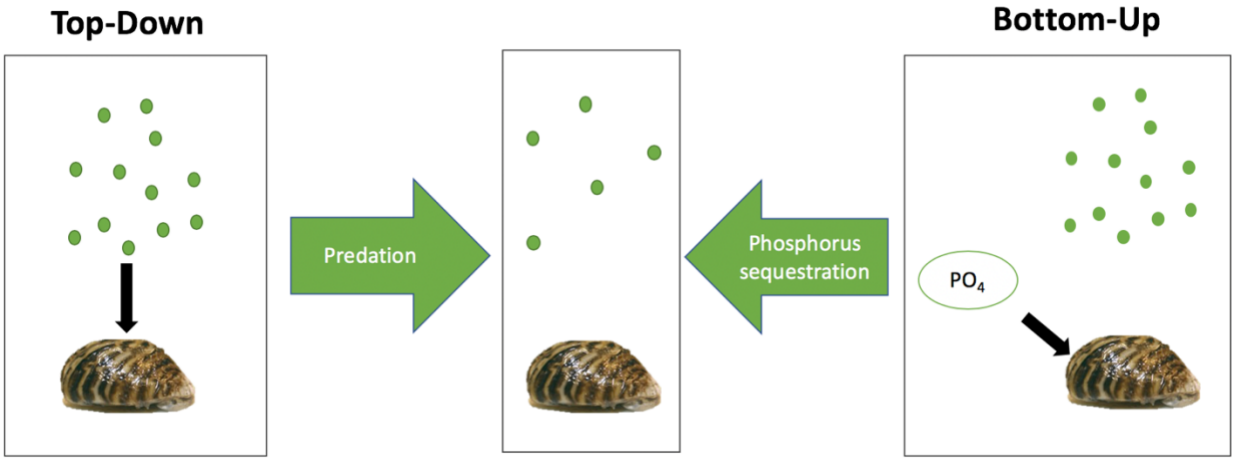


Figure 1-4. Conceptual model of dreissenid regulation of phytoplankton and zooplankton (represented as green dots in each box).

1.3 Dreissenids as a biological driver of HABs in low nutrient lakes

1.3.1 Filtration

Observational and experimental literature attributes the promotion of cyanobacterial blooms to selective filtration by dreissenid mussels. Dreissenids directly affect phytoplankton assemblages via filter feeding as phytoplankton are a primary food source for zebra and quagga mussels (Karatayev et al. 2015). It is well-documented that the presence of dreissenids markedly reduces phytoplankton biomass (Strayer et al. 1999; Higgins and Vander Zanden 2010). Dreissenids are able to selectively feed and can excrete undigested particles as pseudofeces (Vanderploeg 1994). Specifically, zebra mussels selectively rejected colonies of toxin producing *Microcystis aeruginosa* (Vanderploeg et al. 2001, 2013). Zebra mussels were especially inclined to reject those colonies/large masses because mussel feeding tends to be dependent on food particle size (Naddafi et al. 2007). These findings suggest one pathway by which dreissenids can promote cyanobacterial HABs.

Further, filtration by dreissenid mussels has the capacity to indirectly increase light penetration.

1.3.2 Nutrient alteration and redistribution

Dreissenids may indirectly influence formation of HABs by altering nutrient availability and spatial distribution (Williamson and Ozersky 2019). Dreissenids can change the N:P in the water column. Naddafi et al. (2008) found that zebra mussels reduced P availability from June to August by enhancing C:P and N:P ratios in seston, potentially leading to P limitation and reducing food quality and energy transfer efficiency. Dreissenid mussel invasions are also associated with changes in energy production from the pelagic region to the benthic littoral zone (Cecala et al. 2008; Mayer et al. 2013). This phenomenon is called benthification. Depletion of P

from the pelagic zone is well-described by the "nearshore phosphorus shunt" proposed by Hecky et al. (2004); nearshore druses of dreissenids capture allochthonous input via filter feeding, disallowing nutrients to be distributed to the open water. The outcome of these stoichiometric changes combined with nutrient benthification presents a competitive advantage to those buoyant cyanobacteria taxa in low-nutrient lakes (e.g., *Microcystis*).

1.4 Citizen Science

1.4.1. History and citizen science in New York State

Citizen science is the recruitment of non-scientists to collect high-quality, long-term ecological data (Bhattacharjee 2005). Citizen science has become a growing source of data for many disciplines of science, and is increasingly used by scientists, lake managers, and stakeholders to gather valuable long-term information about freshwater systems (Miller-Rushing et al. 2012; Lottig et al. 2014; Vincent et al. 2017). Examples of successful citizen science programs are reviewed in Bonney et al. (2009); in limnology, Sarnelle et al. (2010) found that water-quality data collected by citizen scientists (CVs) was not more variable than data collected by trained professionals. Silvertown (2009) reviews three main drivers of the expansion of citizen science research. The first driver is the accessibility of technological advancements which allow CVs to quickly and easily disseminate observations and findings; the second is the characteristics of CVs (e.g., little to no labor cost, a broad range of skill sets, and access to modern computational technologies); the third is that the common requirements of funded research projects to do some aspect of public outreach is inherent in citizen science. A successful citizen science program in New York has provided quality data from hundreds of inland lakes for over three decades. The Citizen's Statewide Lake Assessment Program (CSLAP) provides long-term water quality and data on HABs to government, lake associations, stakeholders, and

research scientists (Kishbaugh 1988). It is coordinated by the New York State Department of Environmental Conservation (NYSDEC) and the New York State Federation of Lake Associations Inc. (NYSFOLA). New York State has over 7,500 water bodies, and collecting, analyzing, and understanding water quality data from these lakes is crucial for developing lake management plans, understanding freshwater ecosystems, and disseminating data for researchers. CSLAP consists of lake associations who are interested in collecting data about their lakes. From May through September, CVs take measurements and collect data every two weeks. Volunteers are also asked to report their perceptions of the lake including suspected HABs. These measurements and reports, in conjunction with lab-analyzed samples, help the NYSDEC and NYSFOLA meet the three main objectives of CSLAP: 1) collect water chemistry data for lakes; 2) identify problems in lakes and any major changes in water quality; and 3) provide education and outreach to the public regarding lake science (NYSDEC 2019).

1.4.2 Monitoring and sampling dreissenid mussels

Citizen science data has helped document and track geographic distributions of invasive species, but long-term data on invasive species population within a system is still needed. Advances in invasive species monitoring (e.g., New York's *iMapInvasives* program, Partnerships for Regional Invasive Species Management) allow users (including CVs, researchers, and governmental organizations) to report invasive species like terrestrial and aquatic plants and animals. In fact, information on dreissenid invasion used in this body of research was taken from reports documented in the *iMapInvasives* database. These reports rely on the will of CVs to report observations. Currently in New York, there is no coordinated effort to monitor for dreissenids in uninvaded lakes. Furthermore, data on long-term dynamics of dreissenids in invaded systems is not readily available. The prior literature presented (Vanderploeg et al. 2001,

2013; Raikow et al. 2004; Knoll et al. 2008; Sarnelle et al. 2010) suggests a causative link between dreissenids and HABs and therefore warrants the need for more extensive and long term dreissenid data for lakes in New York State.

1.5 Research Motivation and Objectives

The presence of invasive dreissenid mussels is suggested as a causal factor of HABs, especially in low-nutrient lakes where typical factors (i.e., high nutrients) that lead to HABs are not present. I wanted to examine the differences in water quality and HAB parameters between low-nutrient lakes with and without dreissenids using CSLAP data. Furthermore, I wanted to see if there was an easy method for CVs to use that would help lake associations and managers collect data on dreissenid mussels, including monitoring for dreissenids in uninvaded lakes at risk of invasion due to proximity to invaded systems. I used a long-term water quality dataset (CSLAP) for oligotrophic and mesotrophic lakes in New York State to evaluate differences in water quality and HAB parameters as a result of dreissenid invasion. An additional group of 10 CSLAP lakes was used to test a methodology for detecting and tracking dreissenids. I used this data to attempt to:

1. Describe how low nutrient lakes changed after dreissenid invasion (Chapter Two)

2. Describe differences among water quality parameters, including HAB frequency and microcystin concentration, between low-nutrient lakes with and without dreissenid mussels. (Chapter Two)

3. Evaluate if and how the effects of eutrophication (measured by TP and chlorophyll-a) on microcystin concentrations varies between invaded and uninvaded lakes. (Chapter Two)

4. Design and evaluate citizen-accessible method for detecting and monitoring dreissenid mussels. (Chapter Three)

5. Determine if artificial substrates are suitable for detecting and recruiting dreissenid mussels (Chapter Three)

6. Describe variations in mussel abundance and mussel shell length distributions through the summer. (Chapter Three)

The data and insights collected from this thesis will help inform the impacts of dreissenids on low-nutrient lakes. Because the effects of dreissenids are generally well understood, I hope to specifically elucidate if their role in HABs formation and toxicity in low-nutrient lakes is at play in low nutrient lakes of New York State. The results of these analyses will ideally bring additional attention of lake managers to the effects of invasive species. Further, this body of work could help to inform management practices regarding monitoring for dreissenids pre-invasion and long-term monitoring of dreissenids post-invasion. Main findings and future research directions are summarized in Chapter Four.

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Chapter Two: Using citizen-science data to evaluate the role of dreissenid mussels in harmful algal bloom formation in low-nutrient lakes in New York State, U.S.A.

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2.1 Abstract

Harmful algal blooms (HABs) are often attributed to nutrient enrichment by eutrophication, but HABs in low-nutrient lakes are becoming more prevalent. We sought to evaluate if a biological driver, invasive dreissenid mussels, promoted HABs in lakes of New York State, USA. We used data collected by a citizen science monitoring program to evaluate the effect of dreissenids on long-term water quality and HABs data from low-nutrient lakes. For invaded lakes (n = 8), an analysis of water quality pre- and post-invasion showed Secchi depth, chlorophyll-a, and epilimnetic phosphorus varied significantly post-dreissenid invasion. An analysis conducted on a global low-nutrient lake dataset (n = 68 lakes) found that true color varied significantly between invaded and uninvaded lakes, and that neither chlorophyll-a, microcystin concentrations, nor HABs frequency from open water samples were significantly different between lake types. Rather, the global dataset revealed the importance of lake characteristics (i.e., mean depth, catchment area: surface area, watershed agricultural use (% agriculture)), and water temperature as predictors of lake water quality. A reduced, matched dataset (n = total 16 lakes, 8 invaded, 8 uninvaded) was therefore used to assess dreissenid impacts on water quality and HAB parameters. Using this approach, dreissenids were not important drivers of microcystin concentrations and HABs. Instead, TN:TP was a significant predictor of microcystin concentrations. Finally, we found that total phosphorus significantly influenced open water microcystin concentrations in invaded lakes but not uninvaded lakes. These results deviate from previous findings that showed dreissenid invasion resulted in higher toxin concentrations in low to medium nutrient lakes, and a lack of relationship between microcystin concentration and measures of eutrophication in invaded systems. Lake characteristics (mean depth, catchment to surface area ratio, and % agriculture) and water

temperature were more important predictors of nutrient concentrations and water quality parameters related to HABs than invasion status for a subset of low nutrient lakes of New York State.

2.2 Introduction

Harmful algal blooms (HABs) of cyanobacteria are occurring more frequently both globally and in North America and pose risks to human and ecosystem health (Winter et al. 2011; Brooks et al. 2016). Common genera of cyanobacteria, including *Microcystis*, can produce cyanotoxins such as microcystin (O'Neil et al. 2012). Cyanotoxins have been linked to livestock deaths and dog illnesses (Trevino-Garrison et al. 2015) in addition to ecological, economic, and human health implications in regions affected by HABs (Pimentel 2005; Connelly et al. 2007; Baron et al. 2016).

While HABs have historically occurred absent of human causes (summarized in Hallegraeff 1993), the interaction of eutrophication, anthropogenic land-use changes, invasive species, and climate change promote the formation of HABs at an increased rate in inland surface waters (Anderson et al. 2004; Huisman et al. 2018; O'Neil et al. 2012). Nutrient enrichment, specifically of phosphorus (P) (Schindler 1977; Correll 1998), and nitrogen (N) (Gobler et al. 2016; Newell et al. 2018), are known to control the development of HABs. The stoichiometric availability of total nitrogen (TN) and total phosphorus (TP) influences concentrations of microcystin (Scott et al. 2013). Increased global temperatures and severe weather events exacerbated by anthropogenic climate change both directly and indirectly contribute to HAB formation (Paerl and Huisman 2008; Huisman et al. 2018). The growth rates of some cyanobacteria are maximized at high temperatures; further, the growth rate of cyanobacteria can increase at a steeper rate than the growth rate of other phytoplankton (Thomas and Litchman 2016). Hayes et al. (2020) found that warmer temperatures were positively correlated with microcystin concentrations and resulted in prolonged duration of elevated microcystin concentrations in lakes in southern Saskatechwan, Canada. Increased global temperature leads to

more stable and longer periods of stratification in the water column. Stratification presents a selective advantage for those genera of cyanobacteria that can regulate buoyancy. Buoyant cyanobacteria can shade out other phytoplankton during the day, and access additional nutrients in the hypolimnion at night (Walsby et al. 1997). Severe weather events like short, intense storms cause soil erosion in the watershed, leading to increased nutrient loading (Moss et al. 2017). Nutrient concentrations are further increased because of longer residence times from prolonged droughts in the summer (Paerl and Huisman 2017)

Physical characteristics, including mean depth, lake catchment area to surface area ratio (CA:SA), and watershed agricultural use (% agriculture) can indirectly affect nutrient availability and inputs and therefore susceptibility to HABs. Deeper lakes tend to show lower yields of chlorophyll-a in response to nutrient input than shallow lakes likely because of light-limitation. Nutrients are diluted throughout the entire water column, but only nutrients in the euphotic zone are accessible to primary producers (Phillips et al. 2008) and lakes of larger CA:SA tend to have greater nutrient input (Jacquemin et al. 2019). Agricultural use in a watershed is associated with lake nutrient input; P export from an agricultural watershed is expected to be greater than other land-use types (e.g., forested watershed) (Vaithiyanathan and Correll 1992; Chen and Driscoll 2009).

HABs in the Laurentian Great Lakes basin are most frequent in Lake Erie, the shallowest and most productive Great Lake (Michalak et al. 2013; Ho and Michalak 2017). Lake Erie has frequently experienced HABs dominated by *Microcystis aeruginosa*. Blooms of large spatial extent in 2011 covered nearly the entire western basin, and water column integrated samples for microcystin concentrations ranged from 0.1 μg/L to 8.7 μg/L (Michalak et al. 2013). In 2014, microcystin was detected in the finished drinking water for the city of Toledo, Ohio which

brought increased societal and scientific attention to HABs (Steffen et al. 2015). Michalak et al. (2013) concluded that increased spring precipitation along with long-term agricultural land-use contributed to a marked pulse of allochthonous P into the lake which may have led to the 2011 event. However, high nutrient lakes are not the only lakes experiencing HABs. Increasingly, oligotrophic and mesotrophic systems appear susceptible to HABs (Carey et al. 2012, 2013; Raikow et al. 2004; NYSDEC 2017). HABs in low nutrient (TP < 20 μg/L) lakes are especially perplexing because low-nutrient lakes do not have the expected nutrient conditions necessary for HABs. This suggests another factor may be playing a role in HAB formation in low-nutrient lakes.

Previous studies provide a biological explanation for HABs in low-nutrient systems. Specifically, invasive dreissenid mussels (zebra; *Dreissena polymorpha* and quagga mussels; *Dreissena bugensis rostriformis*) are implicated in HABs formation in low-nutrient lakes (Vanderploeg et al. 2001, 2013; Raikow et al. 2004; Knoll et al. 2008). Invasive dreissenid mussels are considered ecological engineers because they alter the physical, chemical, and biological environment (Coleman and Williams 2002). Dreissenids are obligate filter feeders that reduce overall phytoplankton abundance which can lead to increased Secchi depth, light penetration, and macrophyte growth (Karatayev et al. 1997). True color, a measure of the amount of dissolved substances in the water, can be altered indirectly as a result of these reductions in phytoplankton and other particulate matter. Dreissenid feeding can affect the redistribution of nutrients from offshore pelagic zones to the nearshore benthic zone, increasing primary production in the benthos while reducing productivity (TP, total N (TN), and chlorophyll-a) in the open water (Hecky et al. 2004; Vaughn and Hoellein 2018). There is experimental evidence which shows that dreissenids alter the stoichiometric availability of P and N. Nutrient

regeneration via excretion by dreissenids decreased dissolved inorganic N:P (Benelli et al. 2019); further, Ruginis et al. (2014) demonstrated that the presence of dreissenids significantly affected N and P benthic fluxes either directly (e.g., ammonium excretion) or indirectly (e.g., sediment P release due to anoxic conditions of the benthos). The direction of the change in N:P may be consequential for the composition of the phytoplankton assemblage. Reduced N:P ratios present a selective advantage for cyanobacteria that can fix atmospheric N (Walsby 1985, Huisman et al. 2018). Increased N:P may favor those cyanobacteria who do not fix atmospheric nitrogen, e.g., *Microcystis*, and increased N loading may favor production of microcystin (Van de Waal et al. 2009; Huisman et al. 2018).

Proposed mechanisms of HABs promotion by dreissenid mussels include selective filtration and selective rejection of toxin-producing taxa (Vanderploeg et al. 2001, 2013). In a study of 39 low-nutrient (< 20 μg/L TP) lakes, Knoll et al. (2008) found that lakes invaded with *D. polymorpha* had 3.3 times higher microcystin concentrations than their uninvaded counterparts. Sarnelle et al. (2010) confirmed this trend by finding microcystin concentrations were significantly different between invaded and uninvaded lakes with TP <10 μg/L, with the former having greater microcystin concentration. Furthermore, Sarnelle et al. (2010) found that the effects of eutrophication on microcystin concentrations were limited in invaded lakes. Specifically, chlorophyll-a was not significant predictor for microcystin in either lake type, while P as a limiting nutrient was not significantly correlated with microcystin concentrations in invaded lakes. Therefore, nutrient reduction as a method for reducing HABs may not be effective in low-nutrient lakes that have been invaded by dreissenids. We sought to evaluate if HABs in invaded low-nutrient lakes had higher microcystin concentration than uninvaded low-nutrient lakes in New York State. Much of the literature on dreissenids as promoters of HABs in low-

nutrient lakes comes from Michigan, so we wanted to test hypotheses specific to lakes of New York State, which is in a different ecoregion than Michigan (Omernik and Griffith 2014).

In New York State, water quality monitoring dates back to the 1920s. Sampling efforts have continued through the decades and data on chlorophyll-a, epilimnetic TP (herein referred to as TP), hypolimnetic TP, epiliminetic TN, Secchi depth and true color are routinely collected by the New York State Department of Environmental Conservation (NYSDEC). By the mid 2010s, HABs in New York State were increasingly documented (NSYDEC 2019a). In 2012, 58 water bodies had blooms and in 2016, 174 water bodies had blooms (NYSDEC 2019b). Notably, Skaneateles Lake, an oligotrophic Finger Lake with an established dreissenid population, had an unexpected HAB event in 2017 (NYSDEC 2018). This was especially concerning because unfiltered water from Skaneateles Lake is the primary source of drinking water for the city of Syracuse and surrounding areas.

The Citizen's Statewide Lake Assessment Program (CSLAP) provides long-term water quality data and HABs-related data and is coordinated by the NYSDEC and the New York State Federation of Lake Associations Incorporated (NYSFOLA). Using data from lakes sampled through CSLAP, our study objectives were to 1) use available historical data to quantify lake water quality changes post dreissenid invasion, 2) assess differences in water quality parameters, microcystin concentrations, and HAB frequency between invaded and uninvaded low-nutrient lakes while accounting for variation in lake characteristics (i.e., mean depth, CA:SA, agricultural use in the watershed), and 3) investigate how parameters associated with eutrophication (TP, TN:TP, and chlorophyll-a concentrations) predict microcystin concentrations in uninvaded vs. invaded low-nutrient lakes and whether those relationships are stronger in either lake type. Water quality parameters were expected to significantly change after dreissenid invasion. Specifically,

Secchi depth was expected to increase because of reductions in phytoplankton measured by chlorophyll-a concentration. Comparing invaded lakes with currently uninvaded lakes (Objective two), we expected that invasion status would be a significant predictor for variations in TP, hypolimnetic TP, TN:TP, Secchi depth, and chlorophyll-a. Specifically, Secchi depth was expected to be greater in invaded lakes while chlorophyll-a was expected to be lower in invaded lakes. Due to the nature of CSLAP sampling methodology and the theory of dreissenid littoral benthification of nutrients, TP and hypolimnetic TP were expected to be lower in invaded lakes. Further, we hypothesized that invaded low-nutrient lakes would have more HABs or higher microcystin concentrations. For invaded lakes, it was expected that TP would not be significant predictors for variations in microcystin concentrations, while they would be uninvaded lakes. We expected that increased TN:TP would be positively related to microcystin concentrations in both lake types. Chlorophyll-a was not expected to be a significant predictor of microcystin for either lake type.

2.3 Methods

We sought to evaluate the effect of dreissenid mussels on water quality, HABs frequency, and microcystin concentrations in low-nutrient lakes. We used a historical dataset (1988- 2017) for eight invaded lakes and a five-year (2012-2017) dataset to compare current water quality in invaded (n = 8) and uninvaded (n = 60) lakes from CSLAP. Lakes were considered "uninvaded" for the years before invasion was reported, and "invaded" for the year of invasion and subsequent years. Further details on lake selection are provided below.

2.3.1 Water quality monitoring

Water quality sampling was conducted by lake associations enrolled in CSLAP. Each year, scientists and professionals host training sessions before the sampling season to ensure

citizen volunteers (CVs) collect accurate, reproducible water quality parameter data; CVs follow a standard sampling protocol, and quality assurance/control is performed to further validate the data. Water quality samples are taken bi-weekly from late May to late September. Water samples are collected with a Kemmerer bottle over the deepest point of the lake. These "open water samples" are taken at a depth of 1.5 meters, except in lakes that are shallower than 1.5 meters. Hypolimnetic samples are taken from 1.5 meters above the bottom of the lake in stratified lakes only (n = 54 in our dataset).

The data included in this study were from sampling years 2012-2017 because collection and analytical methods were most consistent during that time period (**Table 2-S1**). Secchi depth, air and water temperature, and various metrics of lake perception are taken in the field and recorded. In the field, aliquots for TP, TN, and calcium are collected and frozen for shipment. Pre-processed samples, chain-of-custody forms, and related paperwork are then shipped in an insulated Styrofoam cooler to a pre-determined lab listed below. For onshore processing of true color, 200 mL of water is vacuum-filtered using a 0.45 μm cellulose nitrate filter and frozen for shipment; the filter is retained and used for cyanotoxin analyses by the Boyer Lab at the State University of New York College of Environmental Science and Forestry (SUNY-ESF) in Syracuse, New York (Boyer 2020). Chlorophyll concentrations from shoreline (SB) samples were analyzed using a FluoroProbe® (bbe Moldaenke 2014). For chlorophyll-a analysis, 6–10 drops of magnesium carbonate ($MgCO_3$) are added to a 0.45 μm cellulose nitrate filter, then 100 mL of sample water are filtered. The filter is folded, wrapped in foil, placed in a tube and frozen for shipment. Chlorophyll-a is analyzed using standard methods (USEPA 445.0, Rev 1.2). True color is estimated by visually comparing water samples to a scaled set of standards created from a platinum-cobalt solution (USEPA 110.2). Water quality analyses were performed at Upstate

Freshwater Institute (UFI) in Syracuse, New York. Calcium analyses were performed at ALS in Rochester, New York.

SB samples were taken when a HAB was visually identified by CVs. Samples were analyzed for total chlorophyll-a, blue-green chlorophyll-a (bbe Moldaenke 2014), and microcystin at SUNY-ESF. In 2012 and 2013, microcystin was analyzed using the protein phosphatase inhibition assay (PPIA) (An and Carmichael 1994). From 2014-2017, microcystin concentration was determined using liquid chromatography mass spectrometry (LC-MS) (Boyer 2007). Volunteers are asked to sample shoreline blooms when they are visually identified by skimming surface water from the densest area of the bloom, therefore variability in sampling technique among CVs likely creates variability in reported chlorophyll-a and microcystin concentrations based on individual perception of the densest bloom area, volume of water collected, and/or submerged depth of collection bottle. No concurrent water quality (e.g., TP, TN, etc) parameters are taken. Therefore, we did not further investigate the SB microcystin data.

Information about the presence of dreissenid mussels and year of invasion was retrieved from *iMapInvasives* (https://www.nyimapinvasives.org/), an online invasive species database managed by the New York Natural Heritage Program.

2.3.2 Lake selection

Between 2012 and 2017, there was a maximum of 165 lakes enrolled in CSLAP. For this study, lakes were categorized and subset by trophic status to include only oligotrophic (annual average TP < 10 μg/L; annual average chlorophyll-a < 2 μg/L; annual average Secchi depth > 5 m) and mesotrophic (10 < TP < 20 μg/L; 2< chlorophyll-a < 8 μg/L; 2 < Secchi depth < 5 m) lakes (n = 140). Then we further subset to include only lakes enrolled for at least three years from 2012 to 2017 (n = 68; **Table 2-S2, Table 2-S3**). We called this final dataset of 68 lakes the

211 "global" dataset (**Table 2-1a**). Of these 68 lakes, 8 had established dreissenid populations
212 between 2012-2017.We used propensity score matching (Sekhon 2011) to create a smaller
213 dataset where the number of invaded and uninvaded lakes was balanced (n = 16; 8 invaded, 8
214 uninvaded). We used mean depth, catchment area to surface area ratio (CA:SA), and percent
215 agricultural use in the watershed (% agriculture) to find matching pairs. We called this dataset
216 the "reduced" dataset (**Table 2-1b**). The matchit function was used to find matching pairs using
217 the package matchit in R (R Foundation for Statistical Computing 2018). We ensured that lake
218 criteria were not significantly different between invaded and uninvaded lakes by using t-tests
219 (mean depth: $t = 1.05$, $p = 0.32$; CA:SA: $t = 0.23$, $p = 0.82$; % agriculture: $t = -0.45$, $p = 0.66$).
220 Stratification was expected to influence water quality variables, so an additional dataset
221 consisting of only lakes that stratify (n = 54) was evaluated separately ("stratified dataset").
222 Similarly, an additional global low TP dataset (n = 47) consisting of lakes with yearly average
223 TP < 11 µg/L was created ("low TP dataset") to attempt to elucidate differences between invaded
224 and uninvaded lakes in a narrow range of annual TP concentrations as shown by Sarnelle et al.
225 (2012). On completion of our study, neither the stratified dataset nor the low TP dataset showed
226 differences from our global and reduced datasets, so only results from the global dataset (n = 68)
227 and reduced dataset (n = 16) will be reported. Model results from the stratified and low TP
228 dataset can be found in the supplementary materials.
229

230 ***2.3.3 Statistical analyses***

231 *Changes in water quality after dreissenid invasion (historical analyses)*

232 To address objective one, we compared water quality data from years before established
233 dreissenid populations (pre-dreissenid) with data from years after populations were established

(post-dreissenid). For the eight invaded lakes in the dataset, historical TP, hypolimnetic TP, TN:TP, chlorophyll-a, and Secchi depth data (1988-2017) were used to compare the effect of dreissenids on water quality. True color was not evaluated for the historical analyses due to significant differences in methods from 1988 to 2017 (pers. comm. Stephanie June, NYSDEC), which were expected to skew results towards greater true color for post-dreissenid years. Microcystin concentrations were not evaluated because this parameter was not analyzed before 2012. We ran a mixed effects model with TP, hypolimnetic TP, TN:TP, chlorophyll-a, and Secchi depth as response variables, invasion status and temperature as fixed effects, and lake and the nested effect of lake in sample year as random effects. All variables except Secchi depth were log-transformed to improve distribution of residuals. We created a linear mixed effects model (function lmer in packaged lme4 in R; R Foundation for Statistical Computing). Residuals of the model were evaluated for normality and heteroscedasticity.

Comparing water quality, HABs parameters, and HABs frequencies between invaded and uninvaded lakes

To address objective two, we used additional linear mixed effect models to evaluate the following response variables: TP, hypolimnetic TP, TN:TP, Secchi depth, true color, open water chlorophyll-a, and open water microcystin. Fixed effects were invasion status (discrete), mean depth (continuous, log-transformed for scale), CA:SA (continuous; log-transformed for scale), percent agriculture (continuous), and water temperature (continuous). For the open water microcystin models, TN:TP was added as a fixed effect. Random effects were lake, sample year, sample month, and the nested effect of lake in sample year. We created a total of 12 models (6 for global dataset, 6 for reduced dataset). When models failed to converge, random effects that

accounted for ~0.0 variation were dropped from the final model (**Table 2-S4**). Residuals of the model were evaluated for normality and heteroscedasticity. Response variables were log-transformed to improved fit as needed.

To further address objective two, NYSDEC threshold concentrations were used to assign bloom statuses, and then frequencies of blooms and high toxin (HT) blooms were computed and compared between invaded and uninvaded lakes only within the global dataset. Events were marked as blooms when concentrations exceeded 25 µg/L blue-green algae chlorophyll; events were marked as HT blooms when concentrations exceeded 25 µg/L blue-green algae chlorophyll and 20 or 10 µg/L microcystin for shoreline bloom or open water samples, respectively (NYSDEC 2019). Then, to evaluate whether the number of blooms and number of HT blooms differed between invaded and uninvaded lakes, a generalized linear mixed effects model from the Poisson family with a log link was used (function glmer; R). The frequency of blooms and HT blooms for each lake in each year was calculated to generate continuous variables. Two separate models were created and either bloom HT bloom frequency was used as the response variable, while invasion status was used as the fixed effect. Lake and the nested effect of lake in year were included as random effects.

Effects of eutrophication on microcystin concentration

To address objective three, TP, TN:TP, and chlorophyll-a were assessed as predictors of microcystin concentrations using linear regression (all variables log-transformed). Only open water samples were used in these analyses because all measurements (microcystin, TP, TN:TP, and chlorophyll-a) were taken concurrently and with standardized methodology.

Table 2-1a. Summary of several parameters for invaded and uninvaded lakes the global dataset. CA:SA = catchment area to surface area ratio; n = number of lakes (Note: lakes can count towards both categories depending on invasion year; invasion status was based on lake-year)

	Uninvaded				Invaded			
Parameter	**n**	**mean**	**range**	**sd**	**n**	**mean**	**range**	**sd**
Secchi depth (m)	62	4.07	1.00–13.60	1.70	8	4.54	1.10–9.10	1.40
Water temperature (C)	62	22.72	7.00–34.00	3.42	8	23.30	10.00–36.00	2.86
True color (PCU)	62	15.79	0.50–100.00	10.73	8	12.95	0.50–55.00	9.25
Calcium (µg/L)	62	11.04	1.53–58.30	9.71	8	28.43	14.30–57.80	11.33
TP (mg/L)	62	0.012	0.0–0.22	0.007	8	0.013	0.004–0.066	0.007
TN:TP	62	42.09	1.08-7936	170.55	8	46.77	0-240.59	41.11
Bottom total phosphorus (mg/L)	48	0.06	0.0–3.91	0.17	8	0.04	0.0–0.37	0.05
Open water total nitrogen (mg/L)	62	0.38	0.0–12.93	0.41	8	0.52	0.0–4.12	0.44
Open water chlorophyll-a (µg/L)	62	3.38	0.05–63.20	3.68	8	2.37	0.05–13.30	1.84
Shoreline bloom chlorophyll (µg/L)	39	2791.20	0.28–74781.25	9683.79	5	2138.20	0.20–31507.50	6226.95
Shoreline bloom microcystin (µg/L)	39	2086.22	0.81–39757.13	7757.75	5	74.93	0.83–361.24	92.45
Open water microcystin (ug/L)	62	1.19	0.16-52.87	5.58	8	0.64	0.33-1.84	0.53
CA:SA	60	16.59	0.74–210.4	30.05	8	32.58	4.5–189.9	63.90

	Uninvaded				Invaded			
Parameter	**n**	**mean**	**range**	**sd**	**n**	**mean**	**range**	**sd**
Mean depth (m)	60	5.75	0.4–21.3	3.86	8	6.33	3.7–9.9	1.92
Agricultural cover (%)	60	6.36	0.0–44.0	11.10	8	21.0	1.00–48.00	15.87

Table 2-1b. Summary of several parameters for invaded and uninvaded lakes in the reduced dataset. CA:SA = catchment area to surface area ratio; n = number of lakes (Note: lakes can count towards both categories depending on invasion year; invasion status was based on lake-year)

	Uninvaded				Invaded			
	n	**mean**	**range**	**sd**	**n**	**mean**	**range**	**sd**
Secchi depth (m)	10	4.14	1.00-8.70	1.47	8	4.54	1.10–9.10	1.40
Water temperature (C)	10	23.21	13.00–33.00	3.35	8	23.30	10.00-36.00	2.86
True color (PCU)	10	14.24	0.50-59.00	8.82	8	12.95	0.50–55.00	9.25
Calcium (µg/L)	10	11.89	1.53–58.30	12.79	8	28.43	14.30–57.80	11.33
TP (mg/L)	10	0.012	0.003–0.1	0.011	8	0.013	0.004–0.066	0.007
TN:TP	10	37.28	5.29-112.64	19.60	8	46.77	0.00-240.60	41.11
Bottom total phosphorus (mg/L)	10	0.03	0.00–0.39	0.06	8	0.04	0.00–0.37	0.05
Open water total nitrogen (mg/L)	10	0.35	0.11–1.24	0.15	8	0.52	0.00–4.12	0.44

	Uninvaded				Invaded			
	n	**mean**	**range**	**sd**	**n**	**mean**	**range**	**sd**
Open water chlorophyll-a (µg/L)	10	3.31	0.05–24.60	3.66	8	2.37	0.05–13.30	1.84
Shoreline bloom chlorophyll (µg/L)	6	1560.47	0.28–8512.50	2245.86	5	2138.20	0.20–31507.50	6226.95
Shoreline bloom microcystin (µg/L)	6	276.07	276.07–276.07	-	5	74.93	0.83–361.24	92.45
Open water microcystin (ug/L)	10	0.52	0.20–1.78	0.39	8	0.64	0.33-1.84	0.53
CA:SA	8	40.38	7.47–210.42	69.17	8	32.58	4.49–189.86	63.90
Mean depth (m)	8	8.49	4.20–21.30	5.52	8	6.33	3.70–9.90	1.92
Agricultural cover (%)	8	17.25	0.00–44.00	17.56	8	21.00	1.00–48.00	15.87

2.4 Results

2.4.1 Changes in water quality after dreissenid invasion (historical analyses)

Dreissenid invasion was found to be a significant predictor for variations in Secchi depth, chlorophyll-a, and TP. Secchi depth increased by ~0.7 m post-invasion (t = -2.05, p = 0.042). This corresponds with model predictions for chlorophyll-a, which showed chlorophyll-a levels were ~82% lower in post-invasion years (t = 6.75, p < 0.0001). TP decreased by ~14% post-invasion (t = -4.89, p < 0.0001). No significant differences in TN:TP or hypolimnetic TP were found pre- and post-invasion.

2.4.2 Comparing water quality, HABs parameters, and HABs frequencies between invaded and uninvaded lakes in New York State (2012-2017)

Invasion status was only a significant predictor for open water true color in the global dataset. For the global dataset, true color was ~50% lower in invaded lakes (**Table 2-2a**). Invasion status was not a significant predictor for any of the models in the reduced dataset (**Table 2-2b**).

Morphological and land use characteristics, and water temperature used as fixed effects in the global dataset were significant predictors for several water quality parameters (**Table 2-2a**). Specifically, CA:SA was a significant predictor for open water true color and Secchi depth. For every 20% increase in CA:SA, true color increased by about 3% and Secchi depth decreased by ~1% (**Table 2-2a**). Mean depth was a significant predictor for TN:TP, open water chlorophyll-a, true color, and Secchi depth. For every 20% increase in mean depth, TN:TP increased by ~2%, open water chlorophyll-a decreased by ~5%, open water true color decreased by 4%, and Secchi depth increased by ~6% (**Table 2-2a**). Percent agriculture was a significant predictor for hypolimnetic TP in the reduced dataset (**Table 2-2b**). For every 1% increase in agriculture,

hypolimnetic TP increased by ~2%. Water temperature was a significant predictor for TN:TP, and chlorophyll-a in the global dataset, and hypolimnetic TP in both the global and reduced dataset. In the global and reduced dataset, hypolimnetic TP decreased by ~3% with each degree increase in water temperature. Water temperature was not, however, a significant predictor for open water microcystin concentrations. TN:TP was a significant predictor for variations in open water microcystin in the both the global and reduced dataset; for every 1 unit increase in TN:TP, open water microcystin decreases by ~1%.

Table 2-2a. Significant model results for the global dataset (n = 68 lakes) using a mixed effects model with invasion status, catchment area to surface area ratio (CA:SA), mean depth (m), percent agriculture (% agriculture), and water temperature in the watershed as fixed effects (for microcystin concentrations, TN:TP was added as a fixed effect). Random effects included year, month, lake, and lake nested in year. Note that the direction of the estimate for continuous variables is increasing, while the direction for the discrete variable 'Invasion Status' is from Invaded to Uninvaded.

Variable	Fixed effect	Estimate	p-value	Direction and Interpretation
log open water TN:TP	log mean depth	0.111	0.037	For every 20% increase in mean depth, TN:TP increases by ~2%
	water temperature	-0.009	0.0424	For every 1 degree increase in water temperature, TN:TP decreases by <1%
log hypolimnetic TP	% agriculture	0.002	.0055	For every 1 unit increase in percent agricultural cover, hypolimnetic TP increases by <1%
	water temperature	-.0025	<0.0001	For every 1 degree increase in water temperature, hypolimnetic TP decreases by <1%
log open water chlorophyll-a (µg/L)	log mean depth	-0.293	0.0027	For every 20% increase in mean depth, open water chlorophyll-a decreases by ~5%
	water temperature	-0.014	0.0232	For every 1 degree increase in water temperature, chlorophyll-a decreases by ~1%
log open water true color (PCU)	Dreissenids	0.369	0.0143	True color is ~46% lower in invaded lakes
	log CA:SA	0.1562	0.0065	For every 20% increase in CA:SA, true color increase by ~3%
	log mean depth	-0.2372	0.0073	For every 20% increase in mean depth, open water true color decreases by ~4%
log Secchi depth (m)	log CA:SA	-0.0713	0.036	For every 20% increase in CA:SA, Secchi depth decreases by ~1%
	log mean depth	0.336	<0.0001	For every 20% increase in mean depth, Secchi depth increases by ~6%
log open water microcystin (µg/L)	TN:TP	-0.0074	0.0198	For every 1 unit increase in TN:TP, open water microcystin decreases by ~1%

Table 2-2b. Significant results from the reduced dataset (n = 16).

Variable	Fixed effect	Estimate	p-value	Direction and Interpretation
log TN:TP	log CA:SA	0.377	0.0007	For every 20% increase in CA:SA, TN:TP increases by ~7%
log hypolimnetic TP	log CA:SA	-0.313	0.0073	For every 20% increase in CA:SA, hypolimnetic TP increases by ~6%
log open water microcystin (µg/L)	TN:TP	-0.0099	0.0478	For every 20% increase in TN:TP, open water microcystin decreases by ~1%

The frequencies of both blooms and HT blooms were not significantly different between invaded and uninvaded lakes in either the global or reduced dataset. Among all years in the global dataset, there were 42 blooms and 20 HT blooms in invaded lakes (n = 8) and 98 blooms and 144 HT blooms in uninvaded lakes (n = 60; **Fig 2-1**).

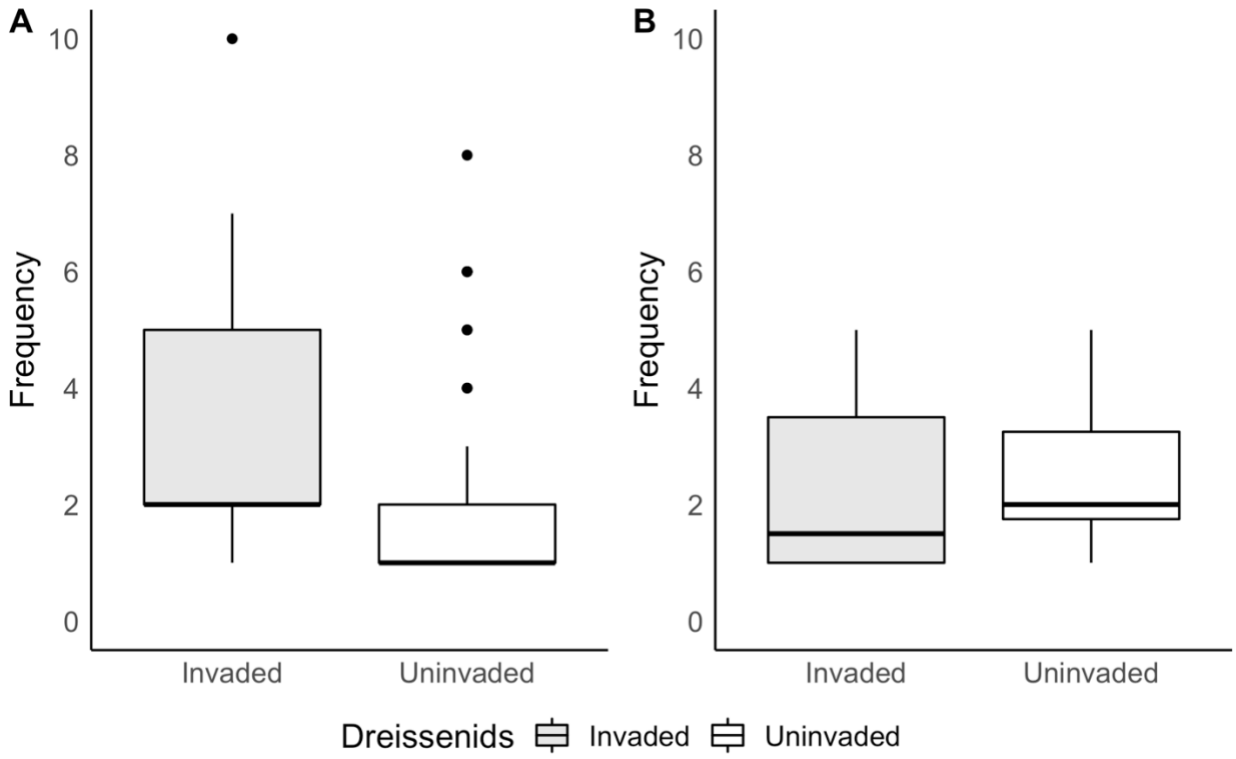

Fig 2-1 (A) 2012 – 2017 Bloom frequencies from invaded and uninvaded lakes (n = 4 invaded, 29 uninvaded) and **(B) 2012-2017** HT bloom frequencies from invaded and uninvaded lakes (n= 2 invaded, n= 4 uninvaded).

2.4.3 Effects of eutrophication on microcystin concentration

We examined TP, TN:TP, and chlorophyll-a as predictors of microcystin concentrations. Overall, TP positively predicted microcystin concentrations; however, the relationship between TP and microcystin was statistically significant only in open water samples from invaded lakes (log microcystin = 8.6+ 4.2 log TP, $R_2 = 0.60$, n = 8, $p = 0.001$) (**Fig 2-2**). No significant relationships between TN:TP and microcystin concentrations were found for either invaded or uninvaded lakes in both open water and shoreline bloom samples (**Fig 2-S1**). Similarly, no significant relationships between chlorophyll-a and microcystin were found for either invaded or uninvaded lakes (**Fig 2-S2**).

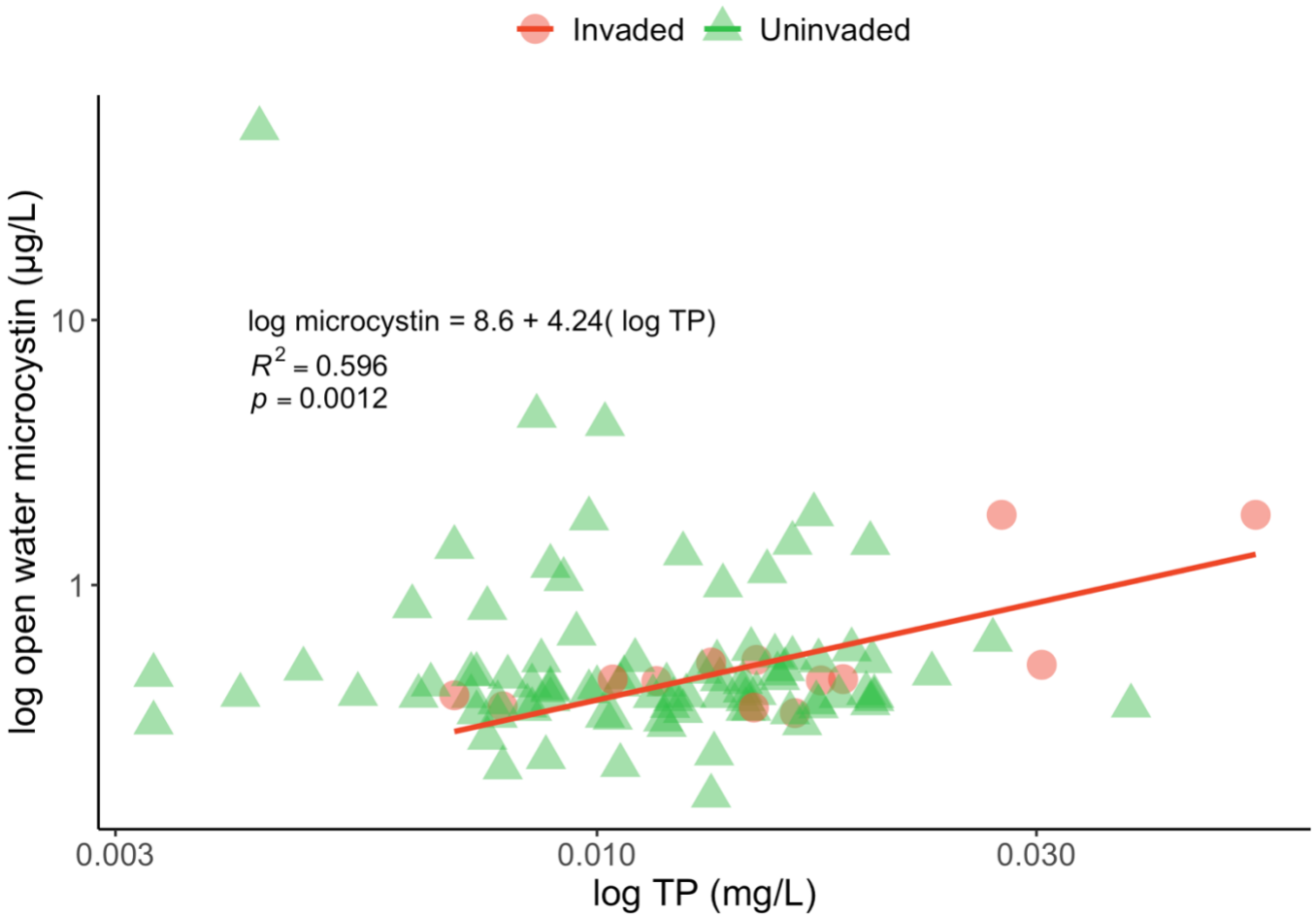

Fig 2-2. Relationship between total phosphorus (TP) and open water microcystin. Red circles and red line- invaded lakes; green triangles- uninvaded lakes. TP is a significant predictor for open water microcystin in invaded lakes only.

2.5 Discussion

We examined low-nutrient lakes that were sampled by New York State's CSLAP citizen science monitoring program to determine how dreissenid invasion influenced water quality and HABs. Historical data comparing pre- and post-invasion showed that dreissenids significantly changed water quality. However, when comparing currently invaded lakes to uninvaded lakes, we found that HABs in invaded lakes neither occurred at greater frequencies nor did they have greater chlorophyll-a or microcystin concentrations than uninvaded lakes. This finding is inconsistent with our hypotheses and previous research that suggested that dreissenid mussels promote toxic HABs in low nutrient lakes (Sarnelle et al. 2010; Vanderploeg et al. 2001). In fact, lake characteristics and water temperature were often significant predictors of water quality parameters. Regression analyses using TP, TN:TP, and chlorophyll-a as predictors of microcystin in open water samples revealed unexpected relationships. TP was positively and significantly correlated with microcystin in invaded lakes, but negatively and not significantly correlated in uninvaded lakes. TN:TP was negatively correlated with microcystin concentrations in invaded lakes and positively correlated in uninvaded lakes and was not significant in either lake type. Our findings suggest that while the impacts of dreissenids are significant and efforts to prevent invasion should continue, the role of dreissenids as promoters of HABs in low-nutrient lakes may be less important than lake characteristics (CA:SA, mean depth, % agriculture), and temperature.

For the eight invaded lakes, Secchi depth was significantly different between pre-dreissenid invasion and post-dreissenid years. Secchi depth increased, on average, by 0.7 m after invasion. Increased Secchi depth is likely a result of decreased primary productivity by phytoplankton and zooplankton, leading to increased water clarity (Karatayev et al. 1997), which

is supported by our finding that chlorophyll-a concentrations were ~82% greater in pre-dreissenid years. The magnitude of the difference in Secchi depth found here is consistent with known impacts of dreissenids on water clarity. Higgins et al. (2008) found that for two morphometrically and physiochemically similar basins in a small Irish lake, Secchi depth was 0.93 m greater for the invaded basin. Though not examined here, increased water clarity after dreissenid invasion should be considered concomitantly with turbidity. For lakes with high turbidity prior to invasion, the expected effect of increased water clarity via dreissenid filtration may be lessened (Higgins and Vander Zanden 2010). In the western and central basins of Lake Erie, water clarity has not increased since dreissenid invasion. In fact water clarity has decreased in these basins, probably as a result of sediment loading (Barbiero and Tuchman 2004).

Dreissenids have been implicated as drivers of changes in or re-distribution of nutrients. In our study, TP was significantly different between pre-dreissenid and post-dreissenid years. We found that TP decreased by ~14%. This finding is supported by prior research on the effect of dreissenids on TP (Higgins and Vander Zanden 2010). A meta-analysis by Higgins and Vander Zanden (2010) found that TP concentrations in both shoreline and open water samples declined by 18–20% following dreissenid invasion. Hecky et al. (2004) proposed an explanatory mechanism of TP reduction in open water as a function of dreissenid invasion, the "nearshore phosphorous shunt" proposes that dreissenids, an organism which primarily inhabits the littoral zone, intercepts allochthonous nutrient inputs and redistributes it to the littoral benthos.

Overall reductions in phytoplankton biomass by dreissenids can indirectly influence true color by decreasing the amount of dissolved organic matter from phytoplankton biological processes. In the global dataset, the presence of dreissenids was a significant predictor for variations in true color only. True color is used to determine water quality resulting from

dissolved substances only (i.e., particulate matter is filtered out before analysis for true color). This is different from perceived color, which can be influenced by suspended particles and algal matter. The color scale used for these analyses is the platinum-cobalt scale (PCU), where lakes with more color have greater true color, and lakes with less color (i.e., clearer) have lower true color. True color was ~46% lower in invaded lakes. In other words, invaded lakes were clearer than uninvaded lakes. This is unsurprising given the effects of dreissenids on water clarity, but to our knowledge, significant changes in true color following dreissenid invasion have not been widely reported elsewhere. True color is generally impacted by nutrient and run-off input from the watershed (Solomon et al. 2015). Dreissenids in the nearshore benthos are thought to capture allochthonous inputs, limiting offshore productivity (Hecky et al. 2004).

Dreissenid presence was not a significant predictor for the other water quality and HABs parameters (hypolimnetic TP, TN:TP, chlorophyll-a, Secchi depth, and open water microcystin) in the global dataset. Prior research showed that dreissenids significantly decreased hypolimnetic TP, TN:TP and chlorophyll-a, while increasing Secchi depth (Fahnenstiel et al. 1995; Makarewicz et al. 2000; Higgins et al. 2007; Higgins and Vander Zanden 2010; Ruginis 2014). However, these studies considered spatial variations within lakes, by taking multiple samples in littoral and pelagic zones. CSLAP open water and hypolimnetic samples are taken only in the pelagic zone, and therefore may limit the potential to detect variations in TP, TN:TP, and chlorophyll-a between invaded and uninvaded lakes. Further, because our study was limited to oligotrophic and mesotrophic lakes (median open water TP = 0.01 mg/L, range: 0.004–0.07), the effect of dreissenids on TP concentrations may be outweighed by environmental factors like allochthonous nutrient loading and temperature. The range of trophic indicators may obscure the effects of dreissenids on water quality and HABs formation and toxicity in low-nutrient lakes.

Sarnelle et al. (2010) used a regression tree analysis to identify TP thresholds at which microcystin concentrations were significantly different between invaded and uninvaded lakes in Michigan. Future research to identify the effects of dreissenids in low-nutrient lakes of New York State might benefit from similar analyses, i.e., finer grouping of trophic indicators (e.g., TP) before comparisons between invaded and uninvaded systems, but our analyses using only those lake-years with TP < µg/L revealed no significant differences between invaded and uninvaded lakes.

Within the reduced dataset, dreissenids were not a significant predictor for either true color or any other water quality parameter. The reduced dataset was created to equalize variations in abiotic characteristics and therefore better capture any disparities between invaded and uninvaded lakes. That invasion status was not a significant predictor for any variable tested in the reduced dataset further supports our findings that invasion status may be a less important driver of variations in water quality and HABs susceptibility in our dataset.

Bloom and HT bloom frequencies were not significantly different between invaded and uninvaded lakes. Further, we found that microcystin concentrations were not significantly different between invaded and uninvaded lakes in either the global or reduced dataset. This finding contrasts with previous findings that found invaded low-nutrient lakes tend to have higher microcystin concentrations (Knoll et al. 2007; Raikow et al. 2004; Sarnelle et al. 2010), though we acknowledge that the sample sizes for each lake type in our study were fewer than those reported in research from Michigan. Dreissenid mussels exhibit a high degree of influence on the systems they inhabit by altering the physical, biogeochemical, and biological environment; the impacts of which are summarized in Higgins and Vander Zanden (2010). Our results suggest a need for more rigorous controlled studies to elucidate if and how dreissenids

might influence HABs formation in low-nutrient lakes in New York State. Vanderploeg et al. (2017) conducted a laboratory study in which mussels were exposed to different strains of *Microcystis*, as well as strains from different sites in the Great Lakes; from this study the authors determined that rejection of *Microcystis* by mussels can be both size- and toxicity- dependent. Extrapolating from lab experiments remains difficult because bloom formation as a result of selective rejection is also dependent on mussel abundance, available nutrients, and intra- and inter- taxa competition (Vanderploeg et al. 2017).

We looked at the relationships between TP and microcystin concentrations, TN:TP and microcystin concentrations, and chlorophyll-a and microcystin concentrations. We found that neither chlorophyll-a nor TN:TP was a significant predictor for microcystin concentrations in either shoreline bloom or open water samples. This relationship held true in both invaded and uninvaded lakes. We found that TP was positively correlated with microcystin in open water samples from invaded lakes and negatively correlated in uninvaded lakes, but the relationship was significant for invaded lakes only, which refutes the theory that dreissenid mussels limit the influence of TP on microcystin as was found in Raikow et al. (2004) and Sarnelle et al. (2010).

Our findings suggest dreissenid mussels alone might not promote HABs in low-nutrient lakes in New York State, as suggested by prior research (Knoll et al. 2007; Raikow et al. 2004; Sarnelle et al. 2010). Dreissenid populations can be highly variable within a lake (Strayer et al. 2019), so future research should include mussel abundance as a continuous variable in HAB forecast models. This would also allow total filtration rates to be estimated, providing further insight into management. We acknowledge that determining lake-wide abundance requires time, funding, and expertise. In the case that no data on lake-wide abundance is available, we consider methods for detecting presence/absence to be sufficient for making inferences about HABs

promotion by dreissenids. Further research is needed to elucidate the most significant factor(s) that contribute to HABs formation and toxicity. We identified four abiotic factors (mean depth, CA:SA, % agriculture, and temperature) that contribute to variations in water quality parameters and microcystin concentrations. We suggest that these abiotic factors, with a particular focus on increased temperatures due to climate change, be used to identify thresholds at which lakes are more susceptible to HABs, while also stressing the individual lake impacts of dreissenid invasion are profound and disruptive.

Citizen-monitoring should continue to be a source of long-term water quality data. Citizen-science has become an integral part of mass data collection across numerous ecological spheres (Silvertown 2009 and Bonney et al. 2009). Sarnelle et al. (2010) found that water-quality data collected by citizen scientists in Michigan was not more variable than data collected by trained professionals. New York State's CSLAP program has provided standardized quality data for decades to lake managers, scientists, and citizens. In recent years, CSLAP has ramped up efforts to collect HABs related data and create platforms to which HABs information can be rapidly disseminated. Current limitations specific to HABs research include a lack of standardized methods for sampling HABs and specifically within CSLAP, the lack of water-quality data during a shoreline bloom sample (i.e., TP and microcystin not collected concurrently). However, analyses presented above show that data from citizen-science can provide insightful information about water quality to lake managers and scientists.

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Chapter Three: Use of artificial substrate to monitor dreissenid populations as a supplement to an existing citizen-science water quality monitoring program

For first submission to: Lake and Reservoir Management

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3.1 Abstract

Dreissenid mussels are a nuisance invasive species capable of altering the physical, chemical, and biological environments that they invade. Monitoring for presence/absence and sampling for long-term population dynamics is imperative for informing lake management decisions regarding prevention and mitigation. New York State has an expansive and informative network of CVs who collect water quality and harmful algal blooms (HABs) data, but do not regularly monitor or sample for dreissenid mussels. We deployed artificial substrates in 10 lakes in New York State to evaluate the efficacy to detect invasive mussels, and to assess how mussel abundance and shell length varied with substrate deployment time length. We found that the average abundance among lakes was greatest with a deployment time length of 16 weeks, while shell length was greatest at a deployment time length of 12 weeks. Abundance and shell lengths were highly variable within individual lakes, suggesting a need for in-lake replication across multiple sites. Overall, we concluded that artificial substrates deployed in this way do not provide accurate enough information about abundance to lake associations because they likely do not capture variation contributed by preferential depth settling and site differences within the same lake; further, our dreissenid abundance estimates differed by more than an order of magnitude with previous work using a more quantitative sampling approach.

3.2 Introduction

Zebra mussels (*Dreissena polymorpha*) were first reported in the Great Lakes region in Lake St. Clair in 1988 (Hebert et al. 1989), followed by the quagga mussel (*Dreissena rostriformis bugensis*) in 1989. Both species are native to the Ponto-Caspian region, and were likely brought to North America via ballast water from shipping vessels (Hebert et al. 1989; Carlton 2008). Dreissenids are considered one of the most aggressive invasive species in freshwater systems and continue to spread globally via anthropogenic activities including shipping channels, reservoir construction, human migration, and changes in environmental regulations (Karatayev et al. 2007). Since their introduction into the Great Lakes, dreissenids have been found in inland freshwater systems across New York State (Benson et al. 2013)

The ability of dreissenids to rapidly colonize new habitat and readily outcompete native unionid mussels is facilitated by dreissenid life histories. Understanding dreissenid ecology is imperative for lake managers who wish to prevent or mitigate the impacts of dreissenid invasion. Zebra mussels require hard, rocky substrate for attachment and are almost exclusively found in littoral waters at depths between 1 and 6 m, though deeper settlement is possible (Burlakova et al. 2006). Quagga mussels are able to colonize soft, silty substrate at greater depths, e.g., between 16 and 50 m, and cooler water temperatures (Karatayev et al. 2015; Nalepa et al. 2010). Generally, zebra mussels are the first to invade a system, followed by quagga mussels (D'Hont et al. 2018). Following quagga invasion, there tends to be a drastic reduction in zebra mussel biomass because of quagga mussels' increased biomass and spatial distribution (Karatayev et al. 2011). Both species are obligate filter feeders and exhibit high filtration rates, leading to drastic reductions in phytoplankton biomass (Nalepa et al. 1999; Noonburg et al. 2003). Dreissenid reproduction is primarily regulated by water temperature (Nalepa and Schloesser 2013) and

characterized by two distinct stages: the first is a calciferous bivalve attached to substrate (though adult dreissenids are motile and can relocate to optimize feeding), and the second is a veliger (Nalepa and Schloesser 2013).

Invasive dreissenid mussels are called “ecological engineers” because their life history affects the physical, biological, and chemical environment (Coleman and Williams 2002). Mussels aggregate to form druses which, at a minimum, are a nuisance and at a maximum can disrupt processes like water treatment by physically clogging water intake valves (Elliot et al. 2005). Mitigation of mussels in industrial water intake facilities is necessary to reduce biofouling (Elliot et al. 2005). Reductions in phytoplankton by mussels leads to increased water clarity and therefore increases the potential for nuisance macrophyte or algal growth (Higgins and Vander Zanden 2010). Dreissenid mussels also cause widescale ecological disruptions and changes. Dreissenid invasion impacts organisms at all trophic levels, from bacteria in the sediment (Frischer et al. 2000) to piscivorous fish (Strayer et al. 2004), reviewed in Higgins and Vander Zanden 2010.

Dreissenids are implicated as a factor in promoting the formation of freshwater cyanobacterial harmful algal blooms (HABs) in freshwater systems (Raikow et al. 2004; Vanderploeg et al. 2013). HABs are increasingly common in North America (Winter et al. 2011; Brooks et al. 2016; Wurtsbaugh et al. 2019). HABs negatively affect recreation, local economy, and human and animal health (Trevin-Garrison et al. 2015; Brooks et al. 2016). Several mechanisms of dreissenid promotion of HABs have been proposed. Dreissenids may alter the nitrogen to phosphorus ratio (N:P) in the water column (Conroy et al. 2005; Gergs et al. 2009; Hamilton et al. 2020). Dreissenids can re-distribute limiting nutrients including carbon (C) to the benthos and promote growth of benthic algae (Hecky et al. 2004). Armenio et al. (2016) found

65 that the benthic algae *Lyngbya wollei* (cyanobacteria) grown in tanks with live dreissenids had
66 significantly higher concentrations of C, N, and P relative to control treatments without
67 dreissenids. In systems where invasive dreissenids co-exist with native unionid mussels, soluble
68 reactive P can be significantly higher in dreissenid-inhabited sediments versus unionid-inhabited
69 sediments (Benelli et al. 2018). Naddafi et al. (2008) found that zebra mussels reduced P
70 availability from June to August by increasing C:P and N:P ratios. Selective filtration by
71 dreissenids directly affects assemblage composition. Vanderploeg et al. 2001 showed that
72 dreissenids can selectively reject large colonies of toxin-producing species. Selective rejection of
73 toxin-producing species is further observed when there is access to a more desirable food source
74 (Vanderploeg et al. 2013). The risk of widespread ecological and HABs impacts from dreissenid
75 invasion necessitates accessibility to management methods to monitor dreissenid populations.
76 The three main stages of invasive species management are prevention, detection, and
77 mitigation or eradication (Mehta et al. 2007). While preventing invasion by dreissenids should
78 remain the priority of lake managers, early detection is imperative for mitigating the impacts of
79 dreissenid invasion. The cost of monitoring for invasive species should be balanced against the
80 cost of mitigation should a species become established (Counihan and Bollens 2017). Early
81 detection of invasive dreissenids is important even if eradication is not practical or possible.
82 Detection of mussels can help lake managers predict changes that might occur as a result of
83 mussel invasion, including increased water clarity (Binding et al. 2015; Geisler et al. 2016),
84 trophic level changes (Barbiero et al. 2018; Gudimov et al. 2015), and macrophyte growth
85 (Vaughn and Hoellein 2018).
86 The impacts of dreissenid invasion on lakes warrant appropriate methods for detecting
87 and sampling dreissenids. Quadrat sampling via SCUBA is one of the most effective and

accurate methods for estimating lake-wide dreissenid abundance (Wisniewski 1974; Mellina and Rasmussen 1993). While experimental designs vary, the basics of this method involve random placement of a quadrat, and a SCUBA diver collects all mussels within that quadrat. Ferguson et al. (2019) suggests that distance sampling along a transect line via SCUBA is also an efficient method for estimating mussel abundance. Though these methods are regarded as the most accurate, they are labor, time, and resource intensive. Ponar grabs along depth-integrated transects can also provide estimation of mussel abundance and spatial dispersion (Marsden 1992). Given the heterogeneous spatial distribution of mussels, this method is particularly susceptible to either overestimation or under-estimation of mussel abundance. Furthermore, grabs can be both time and labor intensive to collect and process. Underwater videography is a novel method for assessing spatial distribution and abundance of dreissenid mussels that can provide valuable data alone, or in conjunction with classic methods including sonar and Ponar grabs (Mehler et al. 2018). A 2015 study from the Laurentian Great Lakes found that when compared with triplicate Ponar grabs, 500-m videography transects captured more area and gave increased precision to dreissenid biomass and abundance estimations (Karatayev et al. 2018). Availability of low-cost cameras and ease of use makes this method ideal for citizen science; however, analysis of video footage for abundance estimations remains time-consuming and requires expert examination (Raoult et al. 2016).

Artificial substrates serve as a method for estimating mussel biomass and abundance (Marsden 1992). This method requires the placement of material for a given amount of time in order to recruit settling veligers and adults. The substrate can then be removed and analyzed for target data. A wide variety of options exist for artificial substrate; mussels preferentially settle on upper versus lower horizontal surfaces and show no preference among materials including wood,

fiberglass, concrete, aluminum, raw steel, but strongly avoided galvanized steel (Marsden and Lansky 2000). Artificial substrates are an easy, low-cost, and accessible method for dreissenid data collection. Developing a standard sampling protocol for dreissenids is important for comparing data among sites and between sampling periods (Marsden 1992; Ferguson et al. 2019). Lake associations and lake managers should consider artificial substrates as a sampling protocol for monitoring and tracking existing dreissenid populations.

After evidence of invasion, lake managers need to understand long-term population dynamics of dreissenid mussels because these dynamics can help determine ecological and economic impacts of invasion. Researchers have long sought to understand and characterize population dynamics of dreissenids in a given system (Burlakova et al. 2006; Karatayev et al. 2014; Karatayev et al. 2015), but consistent trends in population dynamics among all systems are less understood. Strayer et al. (2019) conducted a cross-system analysis of dreissenid population dynamics trends and reported the following findings: 1) populations increase drastically one to two years after initial introduction; 2) quagga mussels invade after zebra mussels, and; 3) quagga mussels tend to outcompete zebra mussels when both species are in a system. Quagga mussels likely outcompete zebra mussels in the long-term because they invest more heavily in biomass and glycogen storage over byssal attachment strength (Balogh et al. 2019). Long-term population dynamics are inherently unique to a given system and along with the general trends in population dynamics discussed above, can be impacted by local ecological drivers like predation (e.g., Barton et al. 2005; Lederer et al. 2008), nutrient inputs, and water temperature (Karatayev et al. 2015).

We tested the use of artificial substrates as a sampling protocol for dreissenid mussels. Substrates were deployed in lakes sampled as part of the Citizen's Statewide Lake Assessment

Program (CSLAP). CSLAP provides long-term water quality and HABs-related data and is coordinated by the New York State Department of Environmental Conservation (NYS DEC) and the New York State Federation of Lake Associations Inc. (NYSFOLA). CSLAP citizen volunteers (CVs) are typically lake association members who live on or near their lake. From May through October, CVs collect bi-weekly water samples, as well as document any notable changes in, or perceptions of, the lake. CVs also help sample and track HABs. Currently, there is no mandated sampling of dreissenids in CSLAP, but CVs are encouraged to report presence or absence of dreissenids in their waterbody.

We evaluated if artificial substrates could be a beneficial addition to this existing citizen science water quality monitoring program. We wanted to determine if artificial substrates could detect and recruit dreissenid mussels by deploying them in both invaded and uninvaded lakes. We also wanted to determine how the amount of time artificial substrate is deployed for (deployment time length) affects mussel settlement (abundance) and shell length. Further, we quantified the effect of invasion time (years since establishment) on overall abundance and shell length of mussels. Artificial substrates were initially deployed in May and it was expected that the greatest abundance and shell length would be found between deployment time lengths of 12 and 16 weeks, corresponding with the warmest part of the year. It was expected that lakes invaded for longer periods of time would have lower recruitment than those invaded more recently because dreissenid populations tend to level out and decrease over time due to resource depletion. We also compared our findings to previous dreissenid research conduct in Song Lake, Honeoye Lake, and Owasco Lake. These previous studies provided more rigorously estimated abundances to which we compared our results to see if artificial substrates provide similar estimations to more traditional methods. Overall, we expected that artificial substrates would be

an accessible method for CVs to use to collect data on dreissenid mussels because it is low-cost, relatively easy, and can be done by CVs who are already involved in a citizen science program.

3.3 Methods

3.3.1 Site selection

For this study, we selected 10 lakes in Central New York State that were sampled as part of CSLAP in 2019 (**Table S3-1**, **Figure 3-1)**. Docks adjacent to properties owned by CVs were used as the sampling site. Lakes were selected based on CVs willingness and dreissenid invasion status. Eight lakes had established dreissenid populations, and two lakes had no documented presence of dreissenids but are highly susceptible to invasion based on their proximity to invaded lakes. Trophic status varied among lakes from mesotrophic to highly eutrophic. We applied trophic classifications to the study lakes based on data from CSLAP that were determined using New York State trophic guidelines (**Table S3-2**). Substrate and macrophyte descriptions were recorded upon initial site visit in May (**Table 3-1**).

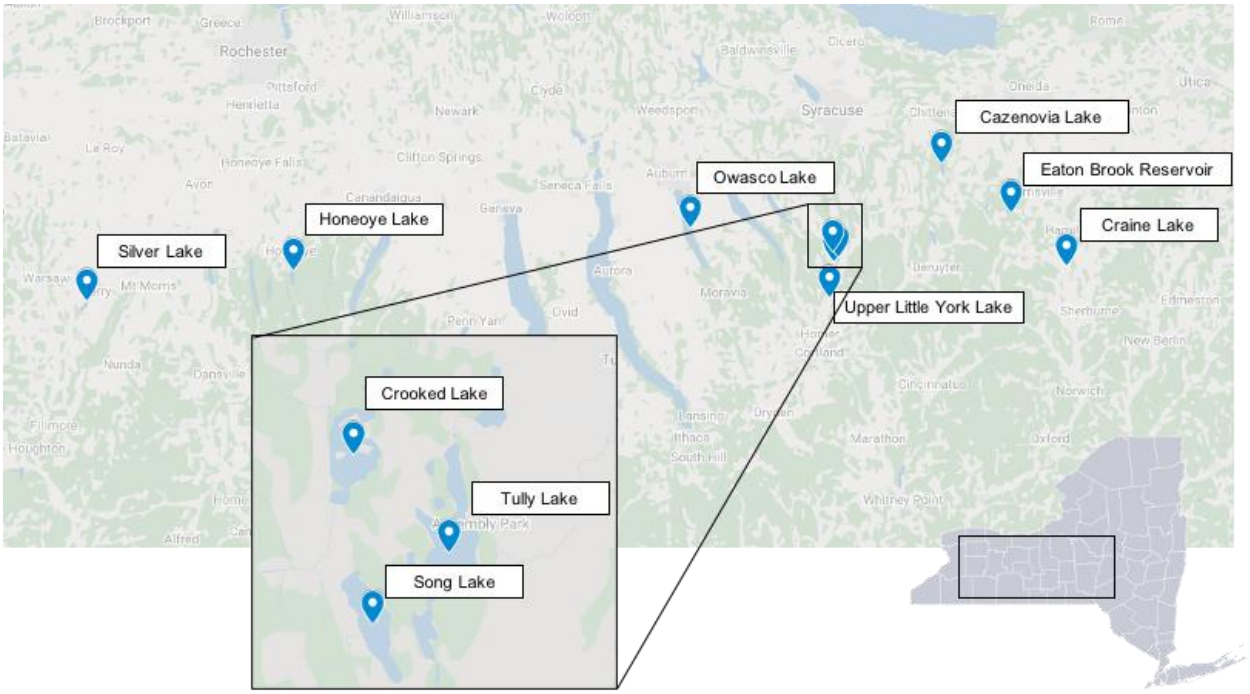

Figure 3-1. Map of lakes where artificial substrates were deployed.

Table 3-1. Substrate deployment site descriptions (location, depth, sediment, and macrophytes)

Lake	Location	Depth (m)	Substrate description	Macrophytes
Honeoye Lake	42°44'31.7"N 77°31'11.7"W	1.32	Small-medium cobble	Little to no macrophytes
Silver Lake	42°41'40.9"N 78°01'31.2"W	1.23	Small pebbles, silty sediments	Little to no macrophytes
Owasco Lake	42°52'57.6"N 76°31'06.7"W	1.18	Cobble substrate, excessive shell litter	No abundant macrophyte growth
Crooked Lake	42°47'11.4"N 76°09'11.8"W	1.5	Small pebbles, silty sediment, excessive leaf litter	Abundant macrophytes
Song Lake	42°46'20.9"N 76°08'50.0"W	0.97	Medium cobble, shell litter	Abundant macrophytes
Tully Lake	42°46'57.6"N 76°08'04.7"W	1.72	Small pebbles, soft sediment, some leaf litter	Abundant macrophytes
Upper Little York Lake	42°42'28.0"N 76°09'16.3"W	0.82	Small-medium cobble	Some macrophytes
Cazenovia Lake Site A	42°56'46.5"N 75°52'36.9"W	0.91	Soft sediment, macrophytes, some shell litter	Little to no macrophytes
Cazenovia Lake Site B	42°57'35.7"N 75°52'41.0"W	0.99	Soft sediment, some macrophytes, some shell litter	Little to no macrophytes
Eaton Brook Reservoir	42°51'52.3"N 75°42'27.5"W	1.5	Large cobble, shell litter, some leaf litter	Little to no macrophytes
Craine Lake	42°45'41.4"N 75°33'22.5"W	0.51	Medium cobble, shell litter, some leaf litter	No macrophytes

3.3.2 Artificial substrate

Five clay bricks were deployed in each lake between late-May and early-June 2019. For Cazenovia Lake, there were two different sites (denoted Cazenovia A and Cazenovia B). Five bricks were placed on the lake bottom and secured with a marine-grade rope to the dock. The depth at which the bricks were situated varied among lakes because water depths at docks differed (mean 1.15m ± 0.35m; **Table 3-1**). Every four weeks, one brick from each lake was removed. All bricks were removed by mid-October for a total of five deployment time lengths. The deployment time length corresponded to the number of weeks the substrate was *in situ*. This methodological design was chosen to examine how mussel abundance and shell length changed through the season, as well as to determine an optimal deployment time length. This method was meant to be feasible for CVs to utilize because the sampling coincided with an existing lake monitoring program.

Bricks were removed from the water, wrapped in foil, and transported back to the lab where they were kept frozen until analysis. After thawing, all visible mussels were removed, and shell length was measured using digital calipers (Thomas 6-inch digital calipers; accuracy: ±0.025 mm). Shell length constituted the greatest length along the ventral side of the mussel. Shell length was taken as an estimate for age. Mussels were identified to the species level. Abundance estimations were calculated as the total number of mussels per brick divided by the available surface area (m^2) of the brick (mussels/m^2). For Cazenovia lake, where we deployed substrates at two different sites, the relative percent difference (RPD) between each deployment time length was calculated.

3.3.3 Summer variations in abundance and shell length

To evaluate variations in abundance through the season, we used a generalized linear mixed effects model in the negative binomial family with a log link using the function glmmTMB in the package glmmTMB in R (R Foundation for Statistical Computing 2018). Mussel abundance was the response variable. For fixed effects we used the deployment time length (number of weeks in water since deployment; continuous variable) and the number of years a lake had been invaded (continuous). Since lakes were sampled repeatedly, lake was used as a random effect. The mixed effects approach then treats individual lakes as a part of a collection of lakes drawn from a population. We expected our data to have an excess of zeros from uninvaded lakes. To check for zero-inflation, we used the testZeroInflation function from the package DHARMa, which compares the distribution of expected zeros against the observed zeros and found that our data was not significantly inflated with zero values. Model assumptions were tested by visually examining residuals QQ plots and residual vs. predicted plots.

To evaluate variations in shell length among deployment time lengths, we used a linear mixed effects model using the function lmer in the package lme4 in R. Shell length (mm) was used as the response variable. Deployment time length was used as the fixed effect (weeks; continuous). Lake was a random effect. Model assumptions were tested by visually examining residuals QQ plots and residual vs. predicted plots. Significance for all statistical analyses was set at $\alpha=0.05$.

3.4 Results

3.4.1 Artificial substrates as a method for detecting and recruiting dreissenid mussels

Artificial substrates that were deployed in all but one invaded lake (Craine Lake) effectively recruited dreissenid mussels through all deployment time lengths. No mussels were

recruited in Craine Lake, though there is an established dreissenid population. No mussels were recruited in either Crooked or Tully lakes where invasions have not been reported.

3.4.2 Variation in abundance and shell lengths

Abundance varied greatly both among lakes and deployment time lengths (**Figure 3-2**). A trend of increasing abundance with deployment time length was observed (**Figure 3-3**). Notable exceptions to this trend were for Honeoye Lake, where the greatest abundance was measured at deployment time length of four weeks, followed by a general decline as deployment time length increased. The other exception was Silver Lake, where abundance increased from 4 to 12 weeks, followed by a between deployment times lengths of 12 and 16 weeks (Figure 3-2). Mussel abundance from all lakes and deployment time lengths ranged from 0 to 2,481 mussels /m^2 with a median value of 916 mussels /m^2.

For Cazenovia A, abundance ranged from 11–1,736 mussels/m^2, and averaged 493 ± 719 mussels/m^2. For Cazenovia B, abundance ranged from 0–2,204 mussels/m^2, and averaged 565 ± 947 mussels/m^2. The RPD between deployment time lengths for the two sites in Cazenovia Lake ranged from 24% to 155%. The most similar abundance for the two sites was found at deployment time length of 16 weeks (Cazenovia A abundance = 1736 mussels /m^2, Cazenovia B abundance = 2204 mussels /m^2, RPD = 24%).

Average abundance across all deployment time lengths trended towards a negative correlation with the number of years a lake has been invaded (z=-0.42, p=0.67; **Figure 3-4**). However, Song Lake, the most recently invaded lake in this study, had lower average mussel abundance across deployment time lengths than lakes invaded earlier. The results of the generalized linear mixed effects model indicated that the mussel abundance varied significantly depending on the deployment time length (z=1.991, p=0.05), but not the number of years a lake

has been invaded (z=-0.42, p=0.67). The model estimated that for every additional week of deployment time, the mean number of mussels recruited increased by 5% (**Table S3-3**).

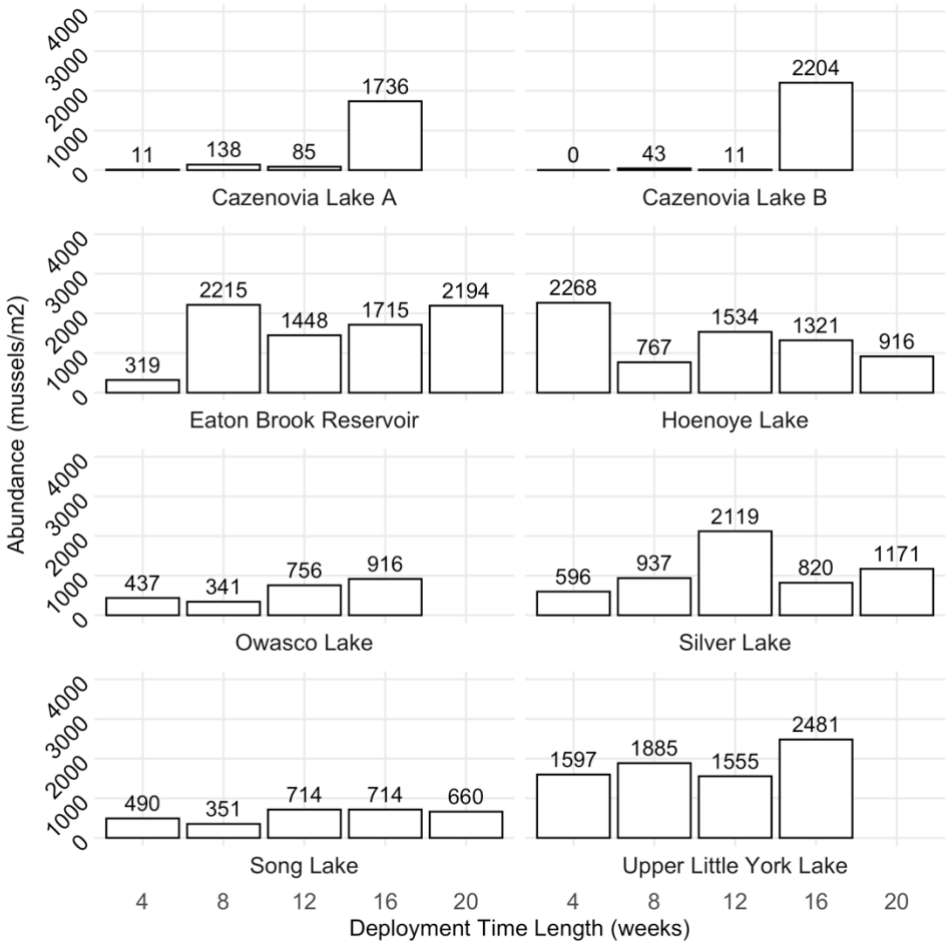

Figure 3-2. Abundance (mussels/m2) at each deployment time length. Values are separated by lake. Substrates from deployment time length of 16 weeks were lost and therefore not reported for both Cazenovia Lake sites and Upper Little York Lake.

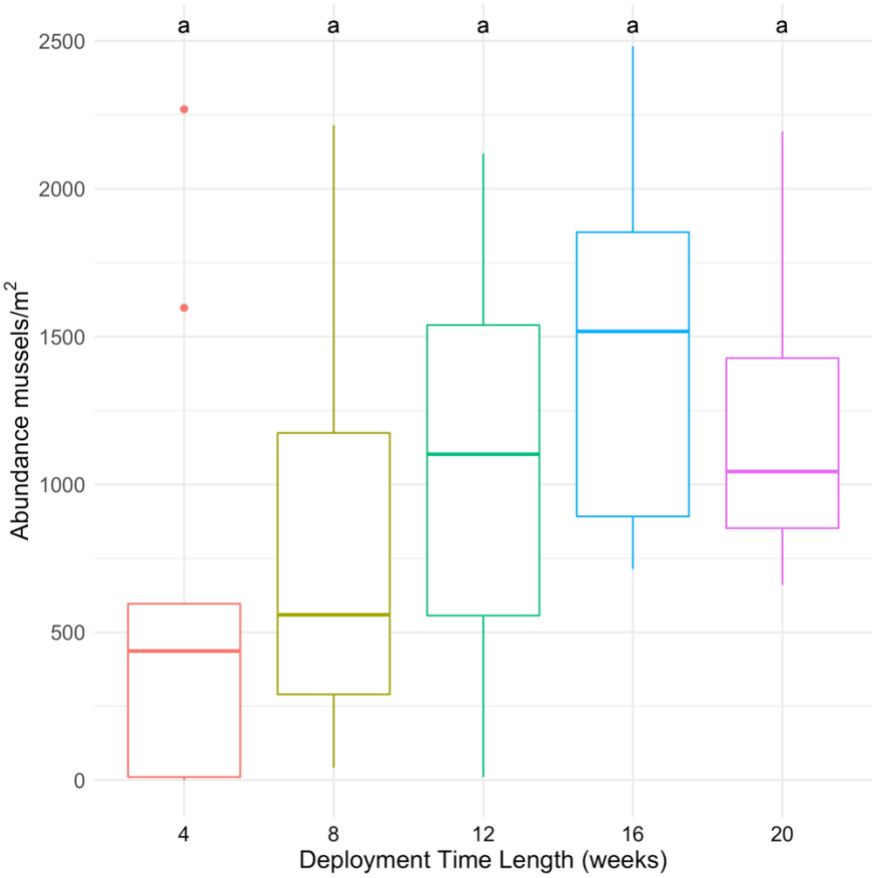

Figure 3-3. Abundances (mussels/m2) for each deployment time averaged across all lakes. Tukey groupings are denoted with a lowercase a and were not significantly different.

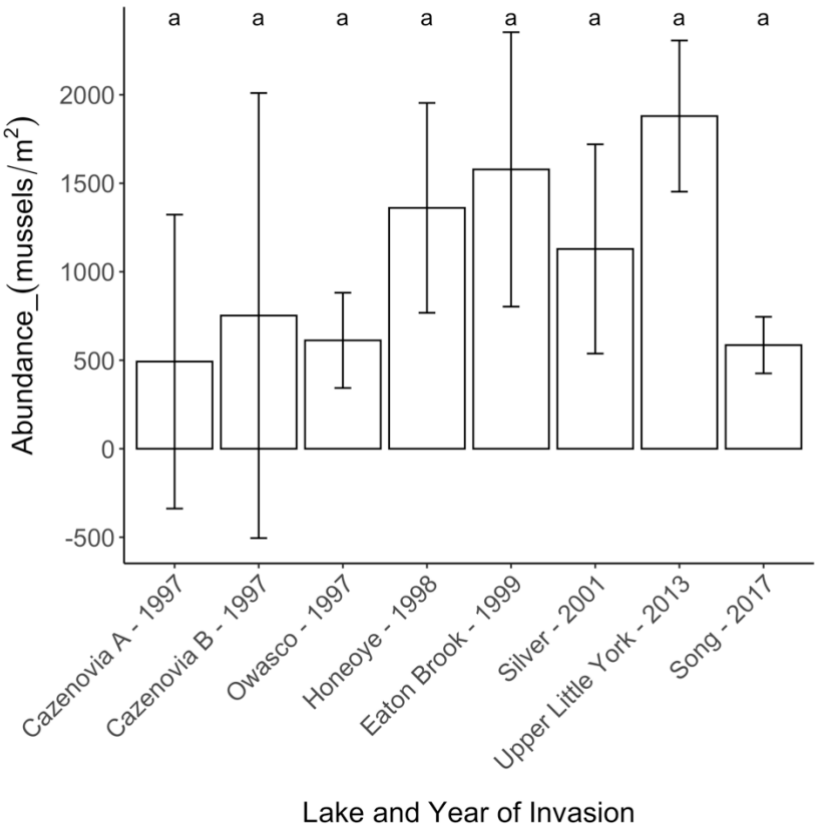

Figure 3-4. Average abundance across all deployment time lengths per lake. Abundance ordered by year of invasion. Error bars are mean ± 1 standard deviation

3.4.3 Shell length distributions

Dreissenid shell lengths among all lakes and deployment time lengths ranged from 0.86 mm (Honeoye Lake) to 20.38 mm (Eaton Brook; **Table 3-2**). Average shell length for each deployment time length ranged from 8.56 ± 3.11 mm (4 weeks) to 9.39 ± 3.62 mm (12 weeks), while average shell length for each lake ranged from 4.43 ± 2.26 mm (Cazenovia Site A) to 10.57 ± 3.56 mm (Silver) (**Table 3-2**). Variations in shell lengths among deployment time lengths were not statistically significant (t= 1.16, *p*=0.25, **Table S3-4**). For three invaded lakes (Cazenovia, Eaton Brook, Honeoye), shell length decreased as deployment time length

increased, while for the other half (Owasco, Silver, and Song, and Upper Little York), shell length increased as deployment time length increased (**Figure S3-1**).

Table 3-2. Summary statistics for shell length (mm).

		Mean	Median	Minimum	Maximum	SD
Deployment Time Length (all lakes)	4 weeks	8.56	8.17	1.88	16.84	3.11
	8 weeks	9.32	9.00	2.23	18.19	3.22
	12 weeks	9.38	9.91	0.86	18.52	3.62
	16 weeks	7.71	7.09	0.99	18.59	4.15
	20 weeks	8.87	8.87	1.06	20.38	4.27
Lake	Cazenovia A	4.66	4.17	1.31	13.09	2.47
	Cazenovia B	4.43	3.99	1.30	16.89	2.26
	Eaton Brook	8.55	8.38	0.99	20.38	4.02
	Honeoye	9.50	10.06	0.86	17.51	3.83
	Owasco	7.22	6.70	0.86	16.57	3.76
	Silver	10.57	10.67	1.11	18.52	3.56
	Song	10.48	10.73	1.06	18.59	2.92
	Upper Little York	8.60	8.49	1.93	16.56	2.62

3.5 Discussion

Clay bricks were deployed in 10 lakes in New York State to evaluate the efficacy of artificial substrates to detect and recruit adult and settling juvenile dreissenids and its ease-of-use for citizen scientists. Further, we investigated the effect of substrate deployment time length on abundance and shell-length distribution. We found that settling juveniles and adults were actively recruited to the artificial substrate. While abundance was highly variable among deployment time lengths and lakes, overall abundance displayed a positive trend with deployment time length (**Figure 3-3**). Shell length distributions were similarly variable among deployment time lengths and lakes. Shell lengths increased with deployment time length in three lakes and decreased with deployment time length in four lakes.

3.5.1 Variation in abundance and shell lengths

We found that while abundance was highly variable (**Figure 3-2**), it generally was positively correlated with deployment time length. The generalized linear mixed effects model estimated that for every additional week of deployment, the mean number of mussels recruited increased by 5%. The median abundance across all deployment time lengths and invaded lakes was 916 mussels/m^2, with the greatest abundance of 2,481 mussels/m^2. Unsurprisingly, abundance estimates from other artificial substrate studies vary greatly. For example, Enders et al. (2019) found abundances ranging from <1,000 to 165,000 individuals per m^2 in the south basin of Lake Winnipeg, Manitoba, Canada. For an amenity lake in Cardiff Bay, Wales, United Kingdom, two studies report differing maximum abundance estimates: Alix et al. (2016) found maximum abundance of settling juvenile mussels to be 54,700 ± 700 per m^2 between 2008 and 2009, while Rolla et al. (2019) found abundances reaching 17,960 individuals per m^2 in Cardiff Bay, United Kingdom. In Lake Erie, abundance estimates varied among basins and depth and ranged from 0 ± 0 to 2,064 ± 1,139 mussels per m^2 (Karatayev et al. 2014). Our abundance estimates were generally lower than other artificial substrate studies. The substrates deployed in this study were exposed to the environment, so predation and excess sunlight may have contributed to reduced recruitment of mussels.

While abundance was generally positively correlated with deployment time length, three lakes did not follow this trend. For Honeoye lake, the greatest abundance of 2,268 mussels/m^2 was found at a deployment time length of 4 weeks; then abundance was reduced to 766 mussels/m^2 at the following deployment time length of 8 weeks. A decreasing trend in abundance as well was found in subsequent deployment time lengths (12, 16, and 20 weeks). A similar trend was found by Alix et al. (2019) for settling veligers in a United Kingdom lake; the greatest abundance occurred in June and was followed by decreasing abundance through the

season. There was an initial increase in abundance with deployment time length in Silver Lake, reaching a maximum abundance of 2,119 mussels/m^2 at 12 weeks deployment time length, and then a decrease in abundance through 16 weeks and 20 weeks deployment time lengths. The shell length distribution for Silver Lake shifted towards larger mussels as total abundance decreased, suggesting that mussels invested more heavily in mass than reproductive efforts. These variations may be representative of the idea that spawning activity of dreissenids is heavily influenced by climatic and ecological factors including water temperature (Karatayev et al. 1998) and planktonic food supplies (Galbraith and Vaughn 2009). The lowest abundance was reported in Song Lake (351–713 mussels/m^2). This finding was in agreement with expected population dynamics for a recently invaded lake (Karatayev et al. 2015). Reports of zebra mussels in Song Lake were first made in 2017. Given that mussels tend to take a few years to reach peak populations (Strayer et al. 2017), it is unsurprising that this recently invaded lake did not exhibit abundances as great as the other lakes. Though Craine Lake has had zebra mussel populations since 2007, no mussels were recruited at any deployment time. This could be a result of the shallow depth of the site, or excess direct sunlight (Karatayev et al. 2015). Given that mussels were recruited in the other invaded lakes, it is likely that the lack of recruitment is a result of deployment error, i.e., site selection.

3.5.2 Lake-wide abundance estimation

We compared abundance estimates from our artificial substrate deployments to abundance estimates from previous research studies in New York State that calculated dreissenid abundance estimates for three of the study lakes, namely Owasco, Song, and Honeoye Lakes (**Table 3-3**). These studies estimated dreissenid abundance using sampling methods expected to have less variation among sites (e.g., ponar grabs at multiple sites, SCUBA collection, and

replicate artificial substrate deployment within a lake). For Song Lake, Caves (2019) found zebra mussel abundances ranging from 308–3,694 mussels//m^2 in shallow (< 2 m) sites across the entire lake. Caves (2019) evaluated the difference in recruitment between the top and the bottom of floating substrate plates and found abundances (304–572 mussels//m^2) comparable to the findings in this study (713 mussels//m^2). For Honeoye Lake, Gilman (2018) found mussel abundances ranging from 0–7,492 mussels//m^2 in the month of July. Abundance estimates from this study ranged from 829–2,454 mussels//m^2 with the lowest abundance detected in July (8 weeks deployment time length) and the greatest abundance detected in mid-June (i.e., 4 weeks deployment time length). Average abundance across all sample times in Honeoye Lake in Gilman (2018) was 2,034 mussels/m^2, compared to our average of 1,361 mussels//m^2. For Owasco Lake, a 2018 survey (Schulz et al., unpublished) found a much greater density of mussels than previous research (Watkins et al. 2007), with dominance of quagga mussels. In sites up to 20 m deep, densities of 15,000 mussels/m^2 were common, with the most densely colonized sites exceeding 30,000 mussels/m^2 (Schulz, personal communication). The artificial substrates deployed for this study were at a much shallower depth, and detected abundances less than 1,000 mussels /m^2, suggesting the need for greater variety of deployment depths to elucidate depth-dependent abundances. We suspect that while abundance estimates from artificial substrates at one site in a given lake might be at least the same order of magnitude as lake-wide abundance, replication at multiple sites within a lake would provide evidence to more accurately estimate lake-wide abundance.

Table 3-3. Dreissenid sampling methods and resulting lake-wide abundance estimations for Owasco Lake, Song Lake, and Honeoye Lake. Present study results are shown under "Present Results".

Lake	Date	Researcher/affiliation	Method	Results	Present Study Results
Owasco Lake	June and October 2007	Watkins et al., Cornell Biological Field Station	Triplicate standard Ponars along 10-meter depth interval transects for sites total.	Lake-wide range: 6–14,049 mussels/m^2	Depth of 1 m; Range: 341–916 mussels/m^2
Owasco Lake	Summer 2019	Schulz et al., SUNY College of Environmental Science and Forestry (personal communication)	SCUBA quadrats collected along depth integral. Specific methods N/A.	Deep sites (20 m), common densities of 15,000 mussels/ m^2	
Song Lake	Summer 2018	Stradder Caves, SUNY Oneonta	Floating artificial substrate plates deployed for from June 1 to September 29. Two deep water (> 6m) and three shallow (< 2m) sites.	Shallow sites range: 308–3,694 mussels/m^2	Depth of 1 m; Range: 351–714 mussels/m^2
Honeoye Lake	Summer 2018	Bruce Gilman, Finger Lakes Community College	Standard Eckman dredge along depth-integrated transect at four sites (n = 12)	Lake-wide range: 0–7,492 mussels/m^2	Depth of 1.3 m; Range: 767–2,268 mussels/m^2

3.5.3 Artificial substrates as a methodology for citizen science

For an uninvaded system, lake managers should be aware of the lake's susceptibility to dreissenid mussels as well as the pathways for invasion. Lake-wide eradication of dreissenids is not currently thought to be possible. Mitigation of druses at water intake facilities and other points-of-interest through the use of biocides and molluscicides is effective (Costa et al. 2011) but is not practical or safe for use in open waters. Because dreissenids are already established in many lakes in New York State, management efforts are focused on reducing secondary spread to uninvaded systems. Dreissenid mussels can be dispersed in two ways: 1) natural dispersion of veligers via downstream movement and 2) anthropogenic overland dispersal via vector-attachment. Evidence for the former has been estimated using 3-D models and shows that planktonic larvae can travel between 1 km to tens of kilometers in merely 2-3 weeks (Beletsky et al. 2017). The latter accounts for a large portion of secondary spread in invaded regions (Kraft et al. 2002; De Ventura et al. 2016). Transportation of boats and other recreational vehicles from one lake to another provides a pathway for veligers to disperse into uninvaded systems, especially zebra mussels because they exhibit a greater attachment rate than quagga mussels (Collas et al. 2018).

Artificial substrates could be an easy and effective way for citizens to collect dreissenid data in their lakes if the sampling design presented here is improved to include additional site and a wider range of depths. Though the design of the artificial substrates can vary greatly among size, shape, position in the water, and material (e.g., Marsden 1992, Martel et al. 1994, Marsden and Lansky 2000, Borcherding and Strum 2002), we propose that a simple substrate composed of a cored clay brick and marine-grade rope secured to any available fixture is

sufficient to recruit dreissenid mussels and, with additional replications in-site and lake-wide, inform citizens and lake managers about the state of dreissenid populations in a system.

The advantages of the methodology presented here are low-cost, require minimal time commitment, utilization of CVs, and enable collection of data about population dynamics of dreissenid mussels. Fabrication of a set of five artificial substrates can be done for as little as $10.00 using materials available at any hardware or home improvement store. Further, removal and measurement of mussels requires no additional materials or advanced tools. Counting methods for this study included only those mussels visible to the naked eye. This method could be used in conjunction with an existing water quality monitoring program. New York State's CSLAP coordinates CVs to sample water bodies bi-weekly from May through October. We believe that recruiting these CVs who are already invested in their lake's health to deploy this methodology would be an easy and ideal way to increase replication and collect high quality dreissenid data. Combining information about dreissenid populations with long-term water quality and HABs data can provide lake managers and associations with important information about lake health. This method could be especially informative in systems where dreissenids are not currently present, but which are susceptible to invasion.

Some consideration of the limitations of this methodology should be taken by managers or associations who wish to implement this method for their lake. While zebra mussels prefer hard substrate, zebra mussels and quagga mussels are able to colonize soft silty substrate and macrophytes (Karatayev et al. 2015). Further, dreissenids can be spatially distributed within a system in non-homogenous fashion (Burlakova et al. 2012; Karatayev et al. 2015), colonizing multiple substrate types including steel, sediment, and nylon; dreissenid settling on macrophytes also presents challenges to accurately estimating abundance. Deploying artificial substrates such

as those described here may therefore underestimate or overestimate lake-wide abundance depending on the amount of available substrate for colonization in the lake. It is therefore imperative that in-lake replications at various locations be deployed to best capture lake-wide abundance. Further, artificial substrates can be re-used for subsequent years to provide information regarding interannual variation of dreissenid populations.

Zebra and quagga mussels are morphologically similar, but their ecological impacts are different. While minimal training would be required, accurate identification of dreissenid species is important. CVs should be trained to recognize differences between zebra and quagga mussels, especially in lakes where zebra mussels are present, but no confirmed populations of quagga mussels have been established. We acknowledge that removing, counting, and measuring every recruited mussel may be time consuming, so CVs may also randomly subset a given surface area and extrapolate from those counts and measurements.

Artificial substrates can be an informative and easy way to sample for dreissenid mussels. We tested an artificial substrate methodology in 10 lakes in New York State. We found that the substrates effectively recruited dreissenids in invaded lakes. Some trends in population dynamics could be elucidated; abundance generally increased with deployment time length, and shell length distribution was highly variable among both deployment time lengths and lakes. We did not detect dreissenids in systems known to be uninvaded, so no conclusion regarding the effectiveness of artificial substrates to detect new invasions can be drawn. We conclude that artificial substrates deployed using this methodology does not provide sufficient information on dreissenid populations.

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Chapter Four: Synthesis and Conclusions

4.1 Review of Research Objectives

There were six main objectives of this research project. I sought to evaluate how dreissenid mussels affect low-nutrient freshwater lakes in New York State using data collected by a citizen-science water quality monitoring program. Using historical water quality data, I analyzed how water quality parameters changed in eight low-nutrient lakes after dreissenid invasion (Objective 1, Chapter 2). Then I compared the current (2012-2017) water quality, HABs parameters, and HABs frequency of those eight invaded lakes to 60 uninvaded lakes (Objective 2, Chapter 2). I then inspected how eutrophication (measured by TP, TN:TP, and chlorophyll-a) affects microcystin concentrations, and whether the relationship is as strong in both invaded and uninvaded lakes (Objective 3, Chapter 2). For Chapter 3, I designed a citizen-science based methodology for detecting and monitoring dreissenid mussels (Objective 4, Chapter 3), then tested the methodology to see if dreissenids were effectively recruited to the artificial substrates (Objective 5, Chapter 3). Using data collected utilizing this methodology, I sought to describe how mussel settling (measured as abundance) and mussel length distribution changes in relation to deployment time (Objective 6, Chapter 3).

4.2 Chapter Two: Using citizen-science data to evaluate the role of dreissenid mussels in harmful algal bloom formation in low-nutrient lakes in New York State, U.S.A.

4.2.1 Main findings

I used historical data to evaluate how a lake changes after dreissenid invasion in eight lakes in New York State. Physical, biological, and biogeochemical changes are expected when a lake is invaded with dreissenid mussels. Increased Secchi depth coupled with reduced

chlorophyll-a concentration is one of the most well-documented examples of the impacts of dreissenid invasion.

I found that dreissenid invasion was a significant predictor for variations in Secchi depth and chlorophyll-a concentration in a pre- post-invasion design. Secchi depth significantly increased and chlorophyll-a concentrations significantly decreased after dreissenid invasion. Secchi depth was found to increase by ~0.7 m after invasion (t = -9.37, $p < 0.0001$). This corresponds with model predictions for chlorophyll-a, which found that chlorophyll-a levels were ~82% lower in post-invasion years (t = 13.31, $p < 0.0001$). It was found that hypolimnetic TP significantly decreased after invasion, validating prior research that suggests hypolimnetic TP in the profundal zone is reduced due to dreissenid retention of allochthonous P inputs.

Using a mixed effects framework, I evaluated how lake characteristics (invasion status, mean depth, CA:SA, and percent agricultural land use in the watershed (percent agriculture)) and water temperature predict variations in open water TN:TP concentration, hypolimnetic TP concentration, Secchi depth, chlorophyll-a concentration, true color, and open water microcystin concentrations. The random effects of lake, sample month, sample year, and the nested effect of lake in sample year were all initially included. Random effects that explained little (<0.0001) variance within a model were dropped. I found that dreissenid invasion was a significant predictor for variations in true color only in the global dataset. Lake and watershed characteristics appeared to explain more variations in water quality parameters. Mean depth was a significant predictor for TN:TP, chlorophyll-a concentrations, true color, and Secchi depth. CA:SA was a significant predictor for true color and Secchi depth. Percent agriculture was a significant predictor for hypolimnetic TP. In light of the importance of lake characteristics on water quality parameters, I used a matching approach to create a reduced dataset (n = 16) with

uninvaded lakes that matched invaded lakes in mean depth, CA:SA and percent agriculture. Using this approach, I found further evidence to support my claim that water quality and HABs parameters are not significantly different between invaded and uninvaded lakes when other lake characteristics are even. Water temperature was a significant predictor for TN:TP, hypolimnetic TP, and chlorophyll-a concentrations. Only TN:TP was a significant predictor for open water microcystin concentrations in both the global and reduced datasets.

I compared bloom and HT bloom frequency between invaded and uninvaded lakes in New York State (2012–2017). I found that neither blooms nor HT blooms occurred at different rates between invaded and uninvaded lakes. This finding was consistent for both the global and the reduced datasets.

The effects of eutrophication on microcystin concentration was evaluated. TP was a significant predictor for microcystin concentrations from open water samples in invaded lakes, but not uninvaded lakes. TN:TP was not a significant predictor for either open water or SB microcystin concentrations in both invaded and uninvaded lakes. Likewise, chlorophyll-a was not a significant predictor for microcystin concentrations from either open water or shoreline bloom samples in both invaded and uninvaded lakes.

4.2.2 Future research

Interestingly, dreissenid invasion status was only a significant predictor for variations in true color. The effects of dreissenid invasion on a lake are well known and well-documented; however, further research into changes in true color might inform a more nuanced effect of dreissenids. Literature documenting true color changes as an effect of dreissenids is limited. It was found that morphological characteristics and water temperature explained more variations in water quality than dreissenid invasion status. This finding might inform best management

practices for lake associations or agencies wishing to prevent or mitigate HABs. I propose that further research is undertaken to identify thresholds for mean depth, CA:SA, percent agriculture, and water temperature to identify lakes that may be most susceptible to HABs. Further, the role of anthropogenic climate change must be explicitly identified as a major contributor of HAB formation. Increased global temperatures lead to longer periods of stratification in deep lakes, which can give a selective advantage to cyanobacteria that can regulate buoyancy. Increased temperature also favors reproduction and productivity in some cyanobacteria and lead to elevated microcystin concentrations. Severe storm pulses directly impact allochthonous nutrient input to lakes by eroding soil and increasing run-off.

New York State's Citizen's Statewide Lake Assessment Program (CSLAP) was the source of the water quality and HABs data used in this research. CSLAP citizen volunteers (CVs) collect high-quality, long-term water quality data. Participants also collect HAB samples and information. While the bi-weekly water quality samples are standardized and quality-controlled, HABs sampling protocol could be further developed. Though the spatial and temporal heterogeneity of HABs presents problems for accurate sampling, deploying a standardized methodology for shoreline HABs sampling and including concomitant analyses of water quality parameters, e.g., TN, TP, temperature, would provide less variable data that could be analyzed for trends and relationships. For water quality parameters regularly sampled, collection at varying sites would further inform spatial variations in nutrient concentrations. This could be particularly informative in lakes invaded by dreissenid mussels because dreissenids have been implicated in spatial re-distribution of nutrients.

4.3 Chapter Three: Use of artificial substrate to monitor population dynamics of dreissenids to supplement an existing citizen-science water quality collection program

4.3.1 Main findings

A citizen-friendly methodology for detecting and monitoring dreissenid mussels was tested in summer of 2019. I deployed five artificial substrates in ten lakes in May 2019. Every four weeks for 20 weeks, one substrate was removed from each lake. Using a mixed effects framework, I identified factors that accounted for variation in mussel abundance through the summer season. It was found that for every additional week of deployment time, the mean number of mussels recruited increased by 5%; for every additional year of invasion, the mean number of mussels recruited increases by 29%. Variations in shell-length distribution through the season were not statistically different between deployment times. Half of sample lakes showed tendencies towards increased shell length as deployment time increased, while the other half tended towards decreased shell length as deployment time increased.

4.3.2 Future research

This study is being extended to the 2020 season. Efforts to improve study design are underway. These efforts include in-site replication of substrates and lake-wide replication of sites. Replication will increase statistical power and accuracy in evaluating differences in mussel settlement through the summer season. Further, lake-wide replication will help inform managers of spatial variations of dreissenid populations. Quality assurance of citizen-collected data should also be considered in future works because of the potential of CVs to miscount or mis-identify dreissenid mussels. Additional efforts could be taken to maximize data collection and inform the different ecological effects of the two dreissenid species. Quaggas can live at greater depths and on different substrate than zebra mussels. Depth-integrated sampling may therefore be necessary to monitor quagga populations. An easy way to incorporate this type of sampling could include attaching artificial substrates to the buoy where CVs sample. Further, it may be necessary to

significantly reduce the frequency of collection or to identify modified methods that can be done with less time. Following the methodology described here, I conclude that the use of this method does not provide sufficient evidence to lake associations.

4.4 Overall Conclusions

Long-term water quality and HABs monitoring is an imperative tool for understanding lake ecology in New York State. CSLAP CVs provide high quality long-term data that informs researchers and lake managers about lake health. Though there is room for improvement, such as standardization of shoreline HABs sampling methods and monitoring dreissenid populations, the data collected helps informs the extremely complicated ecological systems that are unique to each lake. I used CSLAP data to evaluate water quality and HABs parameters in New York State lakes. I found that while the effects of dreissenid mussels were profound in invaded lakes, lake characteristics and water temperature often were better predictors of water quality variations. Further research is needed to elucidate finer-scale effects of dreissenids on HABs and must also consider the interplay of these invasive species with impacts of anthropogenic climate change.

Appendices

Appendix A: Supplementary tables and figures for Chapter Two

Table 2-S1. Description, unit, source, method, and frequency of parameters used in analyses; 2012-2017. More detailed descriptions can be found in the CSLAP Sampling Protocol Guide (NSYFOLA 2015).

Parameter	Unit	Source	Collection/preparation method	Lab method	Frequency of sampling
Secchi depth	m	Field	Secchi disk	*NA*	Bi-weekly
Temperature	C	Field	Analog thermometer	*NA*	Bi-weekly
Catchment to surface area ratio	NA	NYSDEC	*NA*	*NA*	*NA*
Mean depth	m	NYSDEC	*NA*	*NA*	*NA*
Total phosphorus	mg/L	Upstate Freshwater Institute	Kemmerer bottle	SM 18-20, 4500-P E	Bi-weekly
Total nitrogen	mg/L	Upstate Freshwater Institute	Kemmerer bottle	USEPA 353.2, Rev 2.0	Bi-weekly
True color	PCU	Upstate Freshwater Institute	Kemmerer bottle; water vacuum filtered and frozen	USEPA 110.2	Bi-weekly
Calcium	µg/L	ALS	Kemmerer bottle;	USEPA 200.7	Bi-weekly
Chlorophyll-a, extracted	µg/L	Upstate Freshwater Institute	Kemmerer bottle; water filtered onto filter and preserved with $MgCO_3$	USEPA 445.0 Rev. 1.2	Bi-weekly
Bloom chlorophyll (blue-green chlorophyll-a)	µg/L	SUNY ESF	Plastic bottle “scooping” method	bbe Moldaenke 2014	Suspected shoreline bloom events
Microcystin	µg/L	SUNY ESF	Plastic bottle “scooping” method	2012-2013: PPIA (An and Carmichael 1994) 2013-2017: LC-MS (Boyer 2007, 2020)	Suspected shoreline bloom events

Table 2-S2. Average TP (μg/L), chlorophyll-a (μg/L), and Secchi depth (m) across 2012–2017 for lakes (n = 68). Standard deviation denoted as "sd".

Lake	average TP	sd	average chlorophyll-a	sd	average Secchi depth	sd
Augur Lake	21.20	5.38	7.61	5.62	3.1	0.69
Babcock Lake	9.37	2.22	3.17	1.81	4.2	0.84
Big Bowman Pond	14.24	3.63	7.48	4.32	2.1	0.47
Bradley Brook Reservoir	10.05	2.85	1.83	1.06	6.4	1.02
Brantingham Lake	9.23	2.07	5.44	3.31	3.3	0.87
Burden Third Lake	12.57	11.27	3.72	3.50	4.5	1.20
Canada Lake	5.07	1.18	2.03	0.81	4.2	0.70
Cazenovia Lake	19.20	6.97	3.04	1.99	4.2	0.92
Chenango Lake	10.63	3.90	2.48	1.54	4.9	0.96
Craine Lake	13.13	8.40	1.93	1.27	3.2	1.16
Crooked Lake	15.13	2.90	6.15	3.98	3.4	0.74
Cuba Lake	19.27	7.83	7.72	7.62	3.1	1.01
De Ruyter Reservoir	14.45	8.10	2.16	1.01	5.0	1.18
Eagle Lake	7.88	4.98	1.09	0.48	6.9	1.42
Eagle Pond	17.36	13.94	3.47	5.37	1.4	0.12
East Caroga Lake	17.90	21.41	3.51	5.06	3.6	0.60
Eaton Brook Reservoir	11.00	9.36	1.50	0.84	5.6	1.34
Echo Lake	13.20	4.73	4.02	4.15	2.7	0.72
Efner Lake	6.87	2.50	1.93	1.34	4.0	0.81
Forest Lake	11.69	2.78	4.22	3.43	2.4	0.39
Friends Lake	7.76	1.69	3.23	3.52	4.4	0.77
Galway Lake	18.47	24.35	3.11	1.49	3.4	0.69
Geneganslet Lake	10.76	6.78	2.89	2.80	3.1	0.54

Lake	average TP	sd	average chlorophyll-a	sd	average Secchi depth	sd
Glen Lake	8.11	2.41	2.60	2.52	4.1	0.87
Grass Lake	16.08	5.45	2.63	3.22	3.2	0.83
Guilford Lake	22.93	20.92	6.63	6.74	3.1	1.30
Hadlock Pond	7.73	1.75	2.79	1.19	4.8	1.02
Hatch Lake	12.06	2.35	2.92	1.77	5.0	1.30
Hunt Lake	9.79	8.12	2.44	0.90	3.7	0.73
Indian Lake	9.56	2.09	0.87	0.47	6.4	0.89
Jenny Lake	7.00	1.63	3.20	2.18	3.7	0.92
Kasoag Lake	13.28	4.69	5.39	10.39	3.8	0.48
Lake Anawanda	6.92	2.29	1.99	1.57	5.9	1.67
Lake Bonaparte	9.46	7.06	2.03	0.96	4.4	0.64
Lake Devenoge	8.30	1.75	2.93	1.76	3.7	0.59
Lake Forest	13.01	11.34	5.12	6.43	3.3	0.71
Lake of the Woods	7.85	3.11	1.07	0.49	5.5	0.81
Lake Petonia	9.36	2.90	1.83	1.38	5.1	1.21
Lake Placid	4.54	1.50	1.87	0.98	7.7	1.31
Lake Pleasant	7.01	1.22	2.51	1.35	4.5	0.53
Lake Sunnyside	12.90	3.51	2.16	2.33	6.1	0.80
Lincoln Pond	7.45	3.15	1.85	0.80	4.2	0.72
Little Long Pond	31.90	42.55	1.99	1.55	3.0	0.71
Loon Lake	12.17	2.75	2.62	3.23	4.1	0.78
Lorton Lake	19.92	10.87	5.65	5.36	1.9	0.42
Millsite Lake	8.61	3.39	1.56	0.93	7.5	1.00
Oquaga Lake	5.39	1.99	0.95	0.48	8.1	1.34
Otter Lake	14.06	4.35	4.52	2.21	1.5	0.10

Lake	average TP	sd	average chlorophyll-a	sd	average Secchi depth	sd
Panther Lake	15.44	8.40	5.75	3.37	2.1	0.66
Peck Lake	6.55	1.70	3.01	1.54	3.4	0.51
Pleasant Lake	7.39	3.02	2.23	0.91	4.3	0.38
Queechy Lake	8.74	2.35	1.94	2.54	5.6	1.33
Roaring Brook Lake	12.97	3.57	3.69	2.15	2.8	0.69
Round Pond	10.95	2.82	3.68	2.79	2.4	0.50
Sacandaga Lake	9.01	2.66	3.55	1.56	4.5	0.54
Schroon Lake	8.49	7.85	1.64	1.24	4.0	1.03
Sepasco Lake	17.60	4.57	5.15	3.70	3.1	0.65
Silver Lake	9.62	2.83	4.80	3.39	3.9	0.62
Somerset Lake	10.12	2.68	2.21	1.83	4.8	1.29
Song Lake	16.47	4.64	3.99	1.80	3.0	0.68
Spring Lake	12.54	9.80	1.80	2.42	2.5	0.62
Taconic Lake	6.46	2.70	1.34	1.31	4.4	0.73
Tully Lake	14.80	3.80	4.54	2.20	4.2	0.86
Tuscarora Lake	11.38	3.26	2.53	2.43	4.9	1.61
Tuxedo Lake	20.41	9.93	5.88	3.47	3.2	1.22
Upper Little York Lake	13.24	4.78	2.14	1.80	4.2	1.05
Warn Lake	11.73	3.06	4.34	1.77	3.4	0.81
Yankee Lake	18.14	14.40	2.95	1.02	3.2	0.66

Table 2-S3. Description of lakes. Abbreviations: CA:SA = catchment area to surface area ratio; Lat = latitude; Long = longitude; M = mesotrophic; MO = mesoligotrophic; O = oligotrophic; U = uninvaded; I = invaded. * denotes lakes included in the reduced dataset.

Lake Name	Area (ac)	Area (ha)	Watershed Area (ha)	CA:SA	Mean Depth (m)	Watershed Name	Lat	Long	Trophic State	Sampling Years	Invasion Status	Year Invaded
Augur Lake	377	152.8	1134	7.4	3	Lake Champlain	44.4599581	-73.500077	M	1997-2001, 2003-2013, 2015-2017	U	
Babcock Lake	45	18.1	120	6.6	4.6	Upper Hudson River	42.8173862	-73.399494	MO	1987-1995, 1997-2017	U	
Big Bowman Lake	32	13	235	18.1	4.5	Lower Hudson River	42.6487136	-73.488149	M	2013-2017	U	
Bradley Brook Reservoir*	141	57	663	11.6	4.2	Susquehanna River	42.8342769	-75.661294	M	1988-2001, 2011-2014, 2017	U	
Brantingham Lake	327	132.2	658	5.0	8.6	Black River	43.6949159	-75.274089	MO	2001-2010, 2012-2014, 2017	U	
Burden Third Lake	366	148	1130	7.6	3	Lower Hudson River	42.6019432	-73.562028	M	1997-1999, 2003-2011, 2013-2017	U	
Canada Lake*	128	51.8	10900	210.4	21.3	Mohawk River	43.1670634	-74.518339	MO	2001-2010, 2012-2017	U	
Cazenovia Lake*	1184	479.2	2230	4.7	7.1	Seneca/Oneida/ Oswego Rivers	42.9498317	-75.873978	MO	1988-2002, 2004-2008, 2011-2014, 2017	I	1997
Chenango Lake	122	49.2	180	3.7	4.3	Susquehanna River	42.582523	-75.441344	M	2000-2010, 2012-2017	U	
Craine Lake*	26	10.4	50	4.8	3.7	Susquehanna River	42.76052	-75.55785	M	1988-1994, 1996-1998, 2000-2001, 2009-2013, 2015-2017	I	2007
Crooked Lake	115	46.6	903	19.4	4.9	Susquehanna River	42.78741	-76.14978	M	1986-1990, 1993-1998, 2009-2013, 2015-2017	U	
Cuba Lake	454	183.9	6606	35.9	5.2	Allegheny River	42.2505692	-78.292418	M	1986-1988, 1990-1991, 1998-2017	U	
DeRuyter Reservoir*	557	225.3	1011	4.5	7.2	Seneca/Oneida/Oswego Rivers	42.81419	-75.89256	M	1988-2010, 2012-2017	I	2010
Eagle Lake	422	170.9	997	5.8	5.4	Upper Hudson River	43.8803312	-73.586265	O	2000-2017	U	
Eagle Pond	38	15.5	132	8.5	0.4	St. Lawrence River	44.6691553	-74.274282	MO	2009-2013, 2015-2017	U	
East Caroga Lake	346	139.9	300	2.1	3.9	Mohawk River	43.1277264	-74.484093	MO	1990-1995, 2000-2010, 2012-2017	U	
Eaton Brook Reservoir*	269	108.8	1804	16.6	6.2	Susquehanna River	42.86051	-75.6991	MO	1988-2000, 2010-2013, 2015-2017	I	1999
Echo Lake	64	25.9	273	10.5	4.8	Susquehanna River	42.38553	-75.85068	MO	1991-1995, 2002-2010, 2012-2015	U	
Efner Lake	96	38.9	410	10.5	4.2	Upper Hudson River	43.2662239	-73.92851	O	1997-2001, 2012-2017	U	
Forest Lake	19	7.8	85	10.9	2.2	Lower Hudson River	42.7319753	-73.461034	MO	2003-2006, 2009-2011, 2013-2017	U	

Lake Name	Area (ac)	Area (ha)	Watershed Area (ha)	CA:SA	Mean Depth (m)	Watershed Name	Lat	Long	Trophic State	Sampling Years	Invasion Status	Year Invaded
Friends Lake	454	183.9	1440	7.8	4.2	Upper Hudson River	43.625898	-73.844615	M	1991-1995, 2001-2010, 2012-2014, 2017	U	
Galway Lake	518	209.8	2392	11.4	2.6	Mohawk River	43.0306321	-74.075398	M	1990-1997, 2000-2010, 2012-2017	U	
Geneganslet Lake*	102	41.4	1305	31.5	8.5	Susquehanna River	42.51645	-75.77491	MO	1990-2010, 2012-2017	U	
Glen Lake*	320	129.5	2970	22.9	5.6	Lake Champlain	43.36445	-73.67313	MO	1986-1990, 1993-1995, 1997-2017	I	1996
Grass Lake	320	129.5	955	7.4	7.2	St. Lawrence River	44.3344264	-75.714943	M	2004-2011, 2013-2017	U	
Guilford Lake*	70	28.5	213	7.5	8.9	Susquehanna River	42.4130489	-75.499396	M	2004-2008, 2012-2017	U	
Hadlock Pond	275	111.4	2269	20.4	5	Lake Champlain	43.4237	-73.57257	MO	1997-2001, 2011-2015, 2017	U	
Hatch Lake*	134	54.4	354	6.5	6.6	Susquehanna River	42.8346804	-75.677869	M	1988-1996, 1998-2001, 2004, 2011-2017	I	2013
Hunt Lake	134	54.4	560	10.3	3.8	Upper Hudson River	43.2599612	-73.905745	MO	1994-1998, 2002-2013, 2015-2017	U	
Lake Anawanda	38	15.5	80	5.2	6.6	Delaware River	41.85708	-74.963	MO	1988-1993, 1995-1996, 1998-2017	U	
Indian Lake	51	20.7	89	4.3	9.2	Lower Hudson River	41.3731	-73.8877	M	1994-1996, 1998-2001, 2003-2011, 2013-2017	U	
Jenny Lake*	83	33.7	780	23.1	5.5	Upper Hudson River	43.2662018	-73.912673	MO	1994-1998, 2001-2007, 2011-2014, 2017	U	
Kasoag Lake	58	23.3	2269	97.4	2.1	Seneca/Oneida/ Oswego Rivers	43.4727955	-75.923041	M	1991-1995, 2001-2010, 2012-2017	U	
Lake Bonaparte	1286	520.6	4770	9.2	9.4	St. Lawrence River	44.1492639	-75.392673	MO	1988-1992, 1995, 1998-2001, 2007-2017	U	
Lake Devenoge	72	29	52	1.8	8	Delaware River	41.5210716	-74.839509	MO	2014-2017	U	
Lake Forest	45	18.1	308	17.0	1.6	Upper Hudson River	43.367216	-73.790681	M	2001-2010, 2012-2013, 2015-2017	U	
Lake of the Woods	166	67.3	270	4.0	13	St. Lawrence River	44.3155118	-75.727108	O	1994-1995, 1999-2005, 2008, 2015-2017	U	
Lake Placid	2802	1134.4	5140	4.5	8.8	Lake Champlain	44.3222558	-73.973805	O	1991-2017	U	
Lake Pleasant	1440	583	3201	5.5	8.8	Upper Hudson River	43.4775654	-74.377393	O	2014-2017	U	
Lake Sunnyside	26	10.4	63	6.1	4.6	Lake Champlain	43.3753487	-73.639787	MO	1999-2003, 2011-2017	U	
Lincoln Pond	721	291.7	4000	13.7	3	Lake Champlain	44.1431	-73.57318	MO	1997-2001, 2004, 2008-2017	U	
Little Long Pond	13	5.2	98	18.8	2.9	Long Island Sound/Atlantic Ocean	40.9332618	-72.320886	M	2007-2010, 2012-2017	U	
Loon Lake*	166	67.3	602	8.9	6.1	Chemung River	42.4927627	-77.567237	M	1994-2017	U	

Lake Name	Area (ac)	Area (ha)	Watershed Area (ha)	CA:SA	Mean Depth (m)	Watershed Name	Lat	Long	Trophic State	Sampling Years	Invasion Status	Year Invaded
Lorton Lake	45	18.2	1000	54.9	1.4	Lake Ontario	43.503741	-75.89079	M	1990-1994, 2000-2013, 2015-2017	U	
Millsite Lake	505	204.6	420	2.1	12.8	St. Lawrence River	44.2909403	-75.775775	MO	1997-2017	U	
Oquaga Lake	134	54.4	630	11.6	13.9	Delaware River	42.022362	-75.459294	MO	1987-1992, 2002-2017	U	
Otter Lake	282	114	598	5.2	1.4	Black River	43.5917758	-75.11809	M	1992-1996, 2002-2009, 2011, 2013, 2015-2017	U	
Panther Lake	122	49.2	398	8.1	2.6	Seneca/Oneida/ Oswego Rivers	43.3293798	-75.908727	M	1993-1997, 2014-2017	U	
Peck Lake	1369	554.3	4960	8.9	5.8	Mohawk River	43.1146103	-74.412342	MO	1992-1997, 2009-2012, 2014-2017	U	
Petonia Lake*	26	10.4	179	17.2	4.5	Susquehanna River	42.33173	-75.79847	MO	1986-1990, 2001-2017	U	
Pleasant Lake	243	98.4	340	3.5	6.7	Mohawk River	43.1884725	-74.599857	MO	2000-2001, 2003-2011, 2013-2017	U	
Queechy Lake	128	51.8	220	4.2	5.6	Lower Hudson River	42.4069689	-73.415886	MO	1988-1992, 1995, 1997-2017	U	
Roaring Brook Lake	115	46.6	466	10.0	2	Lower Hudson River	41.4392032	-73.807954	M	2009-2013, 2015-2017	U	
Round Pond	13	5.2	57	11.0	2.2	Lower Hudson River	42.6446	-73.43552	M	1991-1995, 2001-2011, 2013-2017	U	
Sacandaga Lake	1593	644.8	5170	8.0	8.5	Upper Hudson River	43.4890591	-74.422423	MO	1987-1991, 1997-2001, 2009-2013, 2017	U	
Schroon Lake	4126	1670.6	136000	81.4	17	Upper Hudson River	43.7395062	-73.794637	MO	1987-1995, 1997-2017	U	
Sepasco Lake	26	10.4	149	14.3	4.2	Lower Hudson River	41.9594681	-73.838532	M	1997-2001, 2003-2011, 2013-2017	U	
Silver Lake	122	49.2	145	2.9	3.7	St. Lawrence River	44.22697	-74.8264	M	1996-2000, 2002-2010, 2012-2017	U	
Somerset Lake	51	20.7	106	5.1	6.1	Delaware River	41.9100855	-75.229	M	1998-2010, 2012, 2014-2017	U	
Song Lake	109	44	255	5.8	4	Susquehanna River	42.7685411	-76.146877	M	2009-2012, 2014-2017	U	
Spring Lake	26	10.4	40	3.8	4	Lower Hudson River	42.6535523	-73.42028	MO	1998-2001, 2007-2011, 2014-2017	U	
Taconic Pond	32	13	115	8.8	4.7	Upper Hudson River	42.7353162	-73.412641	MO	2002-2003, 2006-2007, 2009-2011, 2013-2017	U	
Tully Lake	230	93.2	69	0.7	4.7	Susquehanna River	42.7765192	-76.135285	M	2012-2017	U	
Tuscarora Lake*	307	124.3	1340	10.8	4.3	Seneca/Oneida/ Oswego Rivers	42.8665182	-75.755892	M	1986-2013, 2015-2017	I	2009
Tuxedo Lake*	288	116.6	1480	12.7	8.9	Raritan/Newark Bay	41.1970132	-74.209073	M	2009-2012, 2014-2017	U	
Upper Little York Lake*	102	41.4	7860	189.9	9.9	Susquehanna River	42.703067	-76.156268	MO	2009-2013, 2015-2017	I	2013

Lake Name	Area (ac)	Area (ha)	Watershed Area (ha)	CA:SA	Mean Depth (m)	Watershed Name	Lat	Long	Trophic State	Sampling Years	Invasion Status	Year Invaded
Warn Lake	32	13	269	20.7	3.7	Susquehanna River	42.37451	-75.6464	M	1991-1996, 2001-2010, 2012-2017	U	
Yankee Lake	410	165.8	700	4.2	1.8	Delaware River	41.5866932	-74.559117	M	2006-2011, 2013-2017	U	

Table 2-S4. Final model attributes from generalized linear mixed models

a.

global TN:TP [log]				**reduced TN:TP [log]**			
Predictors	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*
(Intercept)	3.39	3.01 – 3.76	**<0.001**	(Intercept)	3.25	2.35 – 4.15	**<0.001**
Dreissenids [Uninvaded]	-0.02	-0.23 – 0.18	0.834	Dreissenids [Uninvaded]	-0.18	-0.44 – 0.09	0.201
CA:SA [log]	0.05	-0.02 – 0.12	0.139	CA:SA [log]	0.37	0.20 – 0.54	**<0.001**
Mean Depth [log]	0.11	0.01 – 0.21	**0.033**	Mean Depth [log]	-0.28	-0.74 – 0.19	0.245
Percent Agriculture	0.00	-0.00 – 0.01	0.458	Percent Agriculture	0.01	-0.00 – 0.02	0.070
Water Temperature	-0.01	-0.02 – -0.00	**0.041**	Water Temperature	-0.01	-0.03 – 0.00	0.121
Random Effects				**Random Effects**			
σ^2	0.25			σ^2	0.26		
τ_{00} Sample Year*Lake	0.05			τ_{00} Sample Year*Lake	0.05		
τ_{00} Lake	0.06			τ_{00} Lake	0.07		
τ_{00} Sample Month	0.00			τ_{00} Sample Month	0.00		
τ_{00} Sample Year	0.01			τ_{00} Sample Year	0.00		
ICC	0.32			ICC	0.33		
N Sample Year	6			N Sample Year	6		
N Sample Month	6			N Sample Month	6		
N Lake	67			N Lake	16		
Observations	2477			Observations	594		
Marginal R_2 / Conditional R_2	0.028 / 0.344			Marginal R_2 / Conditional R_2	0.256 / 0.500		

b.

global hypolimnetic TP [log]				reduced hypolimnetic TP [log]			
Predictors	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*
(Intercept)	-2.75	-3.73 – -1.78	**<0.001**	(Intercept)	-2.31	-3.30 – -1.33	**<0.001**
Dreissenids [Uninvaded]	0.12	-0.39 – 0.63	0.646	Dreissenids [Uninvaded]	-0.07	-0.38 – 0.24	0.643
CA:SA [log]	-0.01	-0.18 – 0.17	0.931	CA:SA [log]	-0.37	-0.54 – -0.20	**<0.001**
Mean Depth [log]	-0.32	-0.72 – 0.08	0.116	Mean Depth [log]	0.15	-0.34 – 0.63	0.551
Percent Agriculture	0.02	0.01 – 0.03	**0.004**	Percent Agriculture	0.01	-0.00 – 0.02	0.248
Water Temperature	-0.03	-0.04 – -0.02	**<0.001**	Water Temperature	-0.03	-0.05 – -0.01	**<0.001**
Random Effects							
σ^2	0.24			σ^2	0.24		
$\tau_{00\ \text{Sample Year*Lake}}$	0.07			$\tau_{00\ \text{Sample Year*Lake}}$	0.06		
$\tau_{00\ \text{Lake}}$	0.38			$\tau_{00\ \text{Lake}}$	0.07		
$\tau_{00\ \text{Sample Month}}$	0.01			$\tau_{00\ \text{Sample Month}}$	0.02		
$\tau_{00\ \text{Sample Year}}$	0.00			$\tau_{00\ \text{Sample Year}}$	0.01		
ICC	0.65			ICC	0.39		
$N_{\text{Sample Year}}$	6			$N_{\text{Sample Year}}$	5		
$N_{\text{Sample Month}}$	6			$N_{\text{Sample Month}}$	6		
N_{Lake}	53			N_{Lake}	16		
Observations	1480			Observations	442		
Marginal R^2 / Conditional R^2	0.127 / 0.695			Marginal R^2 / Conditional R^2	0.285 / 0.567		

c.

global chlorophyll-a [log]				reduced chlorophyll-a [log]			
Predictors	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*
(Intercept)	1.64	1.03 – 2.25	**<0.001**	(Intercept)	1.21	0.45 – 1.97	**0.002**
Dreissenids [Uninvaded]	-0.13	-0.47 – 0.20	0.438	Dreissenids [Uninvaded]	-0.01	-0.22 – 0.21	0.942
CA:SA [log]	0.04	-0.08 – 0.16	0.543	CA:SA [log]	-0.14	-0.28 – -0.00	**0.045**
Mean Depth [log]	-0.29	-0.48 – -0.11	**0.002**	Mean Depth [log]	0.38	-0.00 – 0.77	0.052
Percent Agriculture	0.00	-0.01 – 0.01	0.477	Percent Agriculture	-0.00	-0.01 – 0.01	0.524
Water Temperature	-0.01	-0.03 – -0.00	**0.023**	Water Temperature	-0.01	-0.03 – 0.00	0.118
Random Effects				**Random Effects**			
σ_2	0.49			σ_2	0.20		
$\tau_{00\ \text{Sample Year*Lake}}$	0.06			$\tau_{00\ \text{Sample Year*Lake}}$	0.02		
$\tau_{00\ \text{Lake}}$	0.22			$\tau_{00\ \text{Lake}}$	0.05		
$\tau_{00\ \text{Sample Month}}$	0.02			$\tau_{00\ \text{Sample Month}}$	0.01		
$\tau_{00\ \text{Sample Year}}$	0.01			ICC	0.30		
ICC	0.39			$N_{\text{Sample Year}}$	16		
$N_{\text{Sample Year}}$	6			$N_{\text{Sample Month}}$	6		
$N_{\text{Sample Month}}$	6			N_{Lake}	6		
N_{Lake}	67						
Observations	2470			Observations	599		
Marginal R_2 / Conditional R_2	0.047 / 0.414			Marginal R_2 / Conditional R_2	0.075 / 0.358		

d.

global true color [log]				reduced true color [log]			
Predictors	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*
(Intercept)	2.27	1.71 – 2.83	**<0.001**	(Intercept)	-5.70	-16.17 – 4.78	0.286
Dreissenids [Uninvaded]	0.37	0.08 – 0.66	**0.013**	Dreissenids [Uninvaded]	-0.13	-4.01 – 3.75	0.948
CA:SA [log]	0.16	0.05 – 0.26	**0.005**	CA:SA [log]	2.27	0.16 – 4.39	**0.035**
Mean Depth [log]	-0.24	-0.40 – -0.07	**0.006**	Mean Depth [log]	4.01	-1.75 – 9.77	0.172
Percent Agriculture	-0.00	-0.01 – 0.01	0.951	Percent Agriculture	0.13	0.00 – 0.26	**0.046**
Water Temperature	-0.01	-0.01 – 0.00	0.147	Water Temperature	0.12	-0.02 – 0.26	0.084
Random Effects				**Random Effects**			
σ_2	0.13			σ_2	19.41		
$\tau_{00\ Sample\ Year*Lake}$	0.07			$\tau_{00\ Sample\ Year*Lake}$	50.83		
$\tau_{00\ Lake}$	0.19			$\tau_{00\ Lake}$	3.70		
$\tau_{00\ Sample\ Month}$	0.02			ICC	0.74		
$\tau_{00\ Sample\ Year}$	0.08			$N_{Sample\ Year}$	16		
ICC	0.73			N_{Lake}	6		
$N_{Sample\ Year}$	6						
$N_{Sample\ Month}$	6						
N_{Lake}	67						
Observations	2505			Observations	602		
Marginal R_2 / Conditional R_2	0.112 / 0.757			Marginal R_2 / Conditional R_2	0.163 / 0.780		

e.

global Secchi depth [log]				reduced Secchi depth [log]			
Predictors	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*
(Intercept)	1.10	0.82 – 1.38	**<0.001**	(Intercept)	1.88	1.23 – 2.53	**<0.001**
Dreissenids [Uninvaded]	-0.09	-0.24 – 0.06	0.256	Dreissenids [Uninvaded]	-0.08	-0.26 – 0.11	0.425
CA:SA [log]	-0.07	-0.14 – -0.01	**0.032**	CA:SA [log]	0.04	-0.09 – 0.17	0.525
Mean Depth [log]	0.34	0.24 – 0.44	**<0.001**	Mean Depth [log]	-0.22	-0.58 – 0.14	0.232
Percent Agriculture	-0.00	-0.01 – 0.00	0.426	Percent Agriculture	-0.00	-0.01 – 0.00	0.346
Water Temperature	-0.00	-0.00 – 0.00	0.205	Water Temperature	-0.00	-0.01 – 0.00	0.487
Random Effects				**Random Effects**			
σ_2	0.04			σ_2	0.06		
$\tau_{00\ \text{Sample Year*Lake}}$	0.01			$\tau_{00\ \text{Sample Year*Lake}}$	0.02		
$\tau_{00\ \text{Lake}}$	0.07			$\tau_{00\ \text{Lake}}$	0.05		
$\tau_{00\ \text{Sample Month}}$	0.00			$\tau_{00\ \text{Sample Month}}$	0.00		
$\tau_{00\ \text{Sample Year}}$	0.00			$\tau_{00\ \text{Sample Year}}$	0.00		
ICC	0.67			ICC	0.56		
$N_{\text{Sample Year}}$	6			$N_{\text{Sample Year}}$	16		
$N_{\text{Sample Month}}$	6			$N_{\text{Sample Month}}$	6		
N_{Lake}	67			N_{Lake}	6		
Observations	2534			Observations	608		
Marginal R_2 / Conditional R_2	0.293 / 0.768			Marginal R_2 / Conditional R_2	0.060 / 0.586		

f.

global open water microcystin [log]			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.53	-1.78 – 2.84	0.651
Dreissenids [Uninvaded]	0.11	-0.33 – 0.54	0.629
TN:TP	-0.01	-0.01 – -0.00	**0.017**
CA:SA [log]	-0.11	-0.27 – 0.05	0.179
Mean Depth [log]	-0.03	-0.07 – 0.02	0.279
Percent Agriculture	0.01	-0.00 – 0.02	0.227
Water Temperature	-0.01	-0.05 – 0.02	0.412
Random Effects			
σ^2	0.18		
τ_{00} Sample Year*Lake	0.09		
τ_{00} Lake	0.01		
τ_{00} Sample Month	0.03		
τ_{00} Sample Year	5.38		
ICC	0.97		
N Sample Year	5		
N Lake	49		
N Sample Month	5		
Observations	96		

reduced open water microcystin [log]			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-0.80	-2.61 – 1.02	0.389
Dreissenids [Uninvaded]	-0.25	-0.70 – 0.20	0.277
TN:TP	-0.01	-0.02 – -0.00	**0.014**
CA:SA [log]	0.04	-0.23 – 0.31	0.795
Mean Depth [log]	-0.47	-1.15 – 0.21	0.172
Percent Agriculture	0.01	-0.00 – 0.03	0.056
Water Temperature	0.04	-0.01 – 0.10	0.120
Random Effects			
σ^2	0.12		
τ_{00} Sample Year*Lake	0.05		
ICC	0.30		
N Sample Year	2		
N Lake	11		
Observations	24		

Marginal R_2 / Conditional R_2	0.006 / 0.968	Marginal R_2 / Conditional R_2	0.384 / 0.571

Table 2-S5. Final model attributes from generalized linear mixed models for the stratified (left) and low TP (right) global models
a.

stratified global TN:TP [log]				**low TP global TN:TP [log]**			
Predictors	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*
(Intercept)	3.17	2.70 – 3.64	**<0.001**	(Intercept)	3.53	3.13 – 3.93	**<0.001**
Dreissenids [Uninvaded]	-0.02	-0.24 – 0.19	0.825	Dreissenids [Uninvaded]	0.02	-0.19 – 0.22	0.875
CA:SA [log]	0.05	-0.03 – 0.13	0.211	CA:SA [log]	0.04	-0.02 – 0.10	0.236
Mean Depth [log]	0.20	0.03 – 0.38	**0.025**	Mean Depth [log]	0.08	-0.02 – 0.19	0.126
Percent Agriculture	0.00	-0.00 – 0.01	0.306	Percent Agriculture	0.00	-0.00 – 0.01	0.517
Water Temperature	-0.01	-0.02 – 0.00	0.145	Water Temperature	-0.01	-0.02 – 0.00	0.127
Random Effects				**Random Effects**			
σ^2	0.26			σ^2	0.23		
$\tau_{00\ \text{Sample Year*Lake}}$	0.05			$\tau_{00\ \text{Sample Year*Lake}}$	0.02		
$\tau_{00\ \text{Lake}}$	0.06			$\tau_{00\ \text{Lake}}$	0.02		
$\tau_{00\ \text{Sample Month}}$	0.00			$\tau_{00\ \text{Sample Month}}$	0.00		
$\tau_{00\ \text{Sample Year}}$	0.01			$\tau_{00\ \text{Sample Year}}$	0.02		
ICC	0.33			ICC	0.20		
$N_{\text{Sample Year}}$	6			$N_{\text{Sample Year}}$	6		
$N_{\text{Sample Month}}$	6			$N_{\text{Sample Month}}$	6		
N_{Lake}	53			N_{Lake}	46		
Observations	1988			Observations	1303		

Marginal R_2 / Conditional R_2	0.042 / 0.355			Marginal R_2 / Conditional R_2	0.017 / 0.214		

b.

stratified global hypolimnetic TP [log]				**low TP global hypolimnetic TP [log]**			
Predictors	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*
(Intercept)	-2.75	-3.73 – -1.78	**<0.001**	(Intercept)	-2.83	-3.63 – -2.04	**<0.001**
Dreissenids [Uninvaded]	0.12	-0.39 – 0.63	0.646	Dreissenids [Uninvaded]	-0.33	-0.79 – 0.13	0.159
CA:SA [log]	-0.01	-0.18 – 0.17	0.931	CA:SA [log]	-0.11	-0.26 – 0.04	0.160
Mean Depth [log]	-0.32	-0.72 – 0.08	0.116	Mean Depth [log]	-0.04	-0.36 – 0.27	0.780
Percent Agriculture	0.02	0.01 – 0.03	**0.004**	Percent Agriculture	0.01	-0.00 – 0.03	0.052
Water Temperature	-0.03	-0.04 – -0.02	**<0.001**	Water Temperature	-0.02	-0.03 – -0.01	**<0.001**
Random Effects							
σ_2	0.24			σ_2	0.17		
τ_{00} Sample Year*Lake	0.07			τ_{00} Sample Year*Lake	0.03		
τ_{00} Lake	0.38			τ_{00} Lake	0.18		
τ_{00} Sample Month	0.01			τ_{00} Sample Month	0.01		
τ_{00} Sample Year	0.00						
ICC	0.65			ICC	0.56		
N Sample Year	6			N Sample Year	6		
N Sample Month	6			N Sample Month	40		
N Lake	53			N Lake	5		
Observations	1480			Observations	848		

Marginal R_2 / Conditional R_2	0.24	Marginal R_2 / Conditional R_2	0.119 / 0.609

c.

stratified global chlorophyll-a [log]				low TP global chlorophyll-a [log]			
Predictors	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*
(Intercept)	1.75	0.99 – 2.52	**<0.001**	(Intercept)	1.48	0.79 – 2.18	**<0.001**
Dreissenids [Uninvaded]	-0.14	-0.47 – 0.20	0.431	Dreissenids [Uninvaded]	0.11	-0.31 – 0.52	0.621
CA:SA [log]	0.05	-0.09 – 0.18	0.505	CA:SA [log]	0.04	-0.09 – 0.17	0.549
Mean Depth [log]	-0.36	-0.67 – -0.05	**0.021**	Mean Depth [log]	-0.41	-0.63 – -0.19	**<0.001**
Percent Agriculture	0.00	-0.01 – 0.01	0.462	Percent Agriculture	-0.01	-0.02 – 0.01	0.355
Water Temperature	-0.01	-0.03 – -0.00	**0.039**	Water Temperature	-0.01	-0.02 – 0.00	0.084
Random Effects				**Random Effects**			
σ^2	0.46			σ^2	0.34		
$\tau_{00\ \text{Sample Year*Lake}}$	0.07			$\tau_{00\ \text{Sample Year*Lake}}$	0.03		
$\tau_{00\ \text{Lake}}$	0.22			$\tau_{00\ \text{Lake}}$	0.14		
$\tau_{00\ \text{Sample Month}}$	0.02			$\tau_{00\ \text{Sample Month}}$	0.00		
$\tau_{00\ \text{Sample Year}}$	0.01			ICC	0.01		
ICC	0.41			$N_{\text{Sample Year}}$	0.36		
$N_{\text{Sample Year}}$	6			$N_{\text{Sample Month}}$	6		
$N_{\text{Sample Month}}$	6			N_{Lake}	6		
N_{Lake}	53				46		
Observations	1984			Observations	1283		
Marginal R^2 / Conditional R^2	0.045 / 0.439			Marginal R^2 / Conditional R^2	0.085 / 0.417		

d.

stratified global true color [log]				low TP global true color [log]			
Predictors	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*
(Intercept)	1.89	1.22 – 2.55	**<0.001**	(Intercept)	2.27	1.48 – 3.06	**<0.001**
Dreissenids [Uninvaded]	0.32	0.04 – 0.60	**0.025**	Dreissenids [Uninvaded]	0.18	-0.29 – 0.66	0.448
CA:SA [log]	0.10	-0.01 – 0.22	0.082	CA:SA [log]	0.13	-0.02 – 0.28	0.099
Mean Depth [log]	0.02	-0.23 – 0.28	0.858	Mean Depth [log]	-0.11	-0.36 – 0.14	0.383
Percent Agriculture	0.00	-0.00 – 0.01	0.382	Percent Agriculture	-0.01	-0.02 – 0.01	0.381
Water Temperature	-0.01	-0.01 – 0.00	0.161	Water Temperature	-0.01	-0.02 – 0.00	0.086
Random Effects				**Random Effects**			
σ^2	0.15			σ^2	0.16		
τ_{00} Sample Year*Lake	0.07			τ_{00} Sample Year*Lake	0.06		
τ_{00} Lake	0.15			τ_{00} Lake	0.19		
τ_{00} Sample Month	0.02			τ_{00} Sample Month	0.04		
τ_{00} Sample Year	0.10			τ_{00} Sample Year	0.09		
ICC	0.70			ICC	0.71		
N Sample Year	6			N Sample Year	6		
N Sample Month	6			N Sample Month	6		
N Lake	53			N Lake	46		
Observations	2013			Observations	1314		
Marginal R_2 / Conditional R_2	0.045 / 0.716			Marginal R_2 / Conditional R_2	0.038 / 0.721		

e.

stratified global Secchi depth [log]			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	1.36	1.01 – 1.71	**<0.001**
Dreissenids [Uninvaded]	-0.09	-0.24 – 0.06	0.251
CA:SA [log]	-0.07	-0.14 – 0.00	0.058
Mean Depth [log]	0.20	0.04 – 0.36	**0.013**
Percent Agriculture	-0.00	-0.01 – 0.00	0.104
Water Temperature	-0.00	-0.00 – 0.00	0.576
Random Effects			
σ^2	0.04		
$\tau_{00\ \text{Sample Year*Lake}}$	0.01		
$\tau_{00\ \text{Lake}}$	0.06		
$\tau_{00\ \text{Sample Year}}$	0.00		
ICC	0.64		
$N_{\text{Sample Year}}$	6		
N_{Lake}	53		
	67		
Observations	2041		
Marginal R^2 / Conditional R^2	0.115 / 0.678		

low TP global Secchi depth [log]			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	1.35	0.95 – 1.75	**<0.001**
Dreissenids [Uninvaded]	-0.08	-0.35 – 0.18	0.530
CA:SA [log]	-0.08	-0.16 – 0.01	0.075
Mean Depth [log]	0.27	0.13 – 0.41	**<0.001**
Percent Agriculture	-0.00	-0.01 – 0.01	0.947
Water Temperature	-0.00	-0.01 – -0.00	**0.018**
Random Effects			
σ^2	0.03		
$\tau_{00\ \text{Sample Year*Lake}}$	0.01		
$\tau_{00\ \text{Lake}}$	0.06		
$\tau_{00\ \text{Sample Month}}$	0.00		
$\tau_{00\ \text{Sample Year}}$	0.00		
ICC	0.72		
$N_{\text{Sample Year}}$	6		
$N_{\text{Sample Month}}$	6		
N_{Lake}	46		
Observations	1322		
Marginal R^2 / Conditional R^2	0.184 / 0.770		

f.

stratified global open water microcystin [log]			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-0.11	-1.44 – 1.23	0.872
Dreissenids [Uninvaded]	0.10	-0.39 – 0.59	0.679
TN:TP	-0.01	-0.01 – 0.00	0.067
CA:SA [log]	-0.09	-0.32 – 0.14	0.453
Mean Depth [log]	-0.02	-0.08 – 0.05	0.590
Percent Agriculture	0.01	-0.01 – 0.02	0.338
Water Temperature	-0.01	-0.05 – 0.03	0.627
Random Effects			
σ_2	0.13		
τ_{00} Sample Year*Lake	0.21		
τ_{00} Sample Month	0.00		
τ_{00} Sample Year	0.05		
ICC	0.67		
N Sample Year	2		
N Lake	38		
N Sample Month	4		
Observations	73		

low TP global open water microcystin [log]			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	1.63	-1.87 – 5.13	0.362
Dreissenids [Uninvaded]	-0.23	-1.45 – 0.99	0.711
TN:TP	-0.01	-0.02 – 0.00	0.278
CA:SA [log]	-0.15	-0.61 – 0.31	0.531
Mean Depth [log]	-0.05	-0.14 – 0.04	0.254
Percent Agriculture	-0.02	-0.08 – 0.03	0.355
Water Temperature	-0.02	-0.08 – 0.05	0.593
Random Effects			
σ_2	0.11		
τ_{00} Sample Year*Lake	0.16		
τ_{00} Lake	0.08		
τ_{00} Sample Year	5.82		
τ_{00} Sample Month	0.01		
ICC	0.98		
N Sample Year	4		
N Lake	25		
N Sample Month	3		
Observations	40		

Marginal R_2 / Conditional R_2	0.064 / 0.694	Marginal R_2 / Conditional R_2	0.006 / 0.983

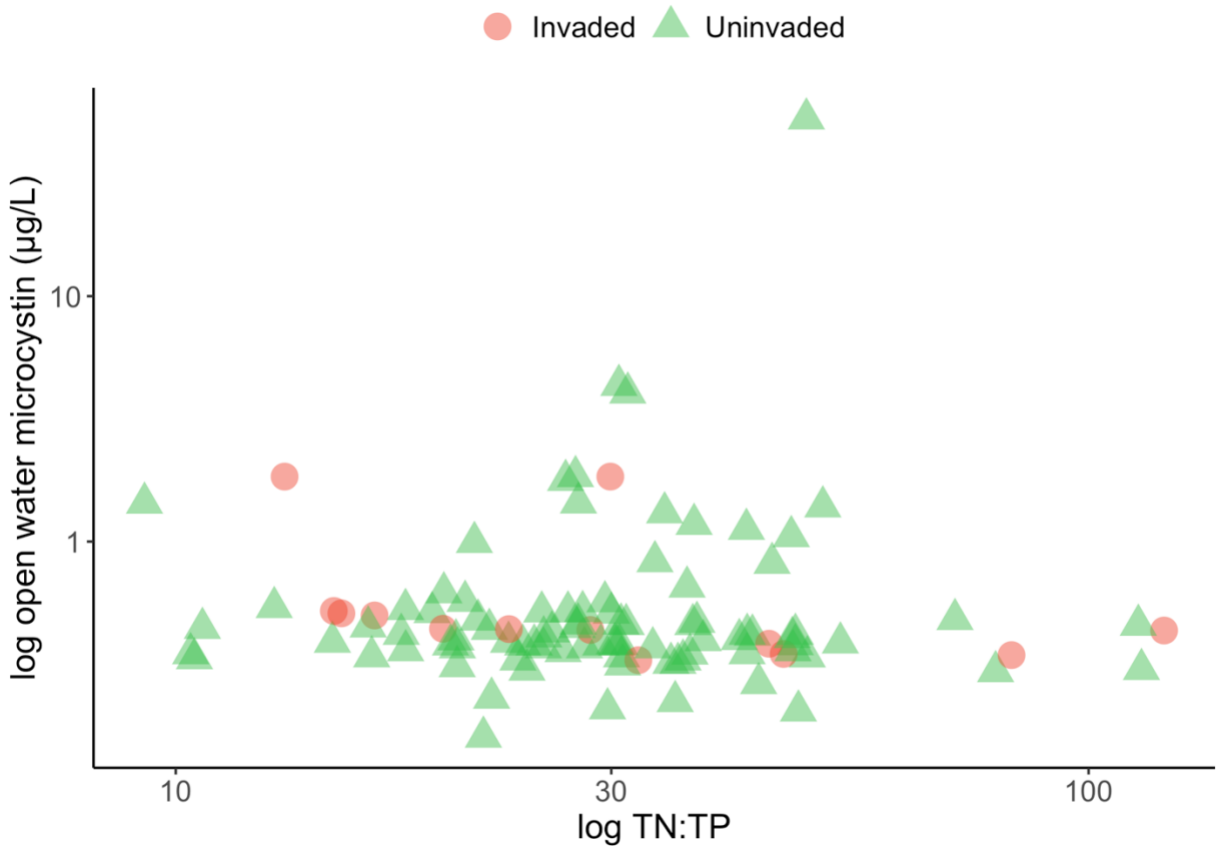


Fig 2-S1. Relationship between TN:TP and open water microcystin. Red circles- invaded lakes; green triangles- uninvaded lakes. TN:TP was not a significant predictor for open water microcystin in both invaded and uninvaded lakes.

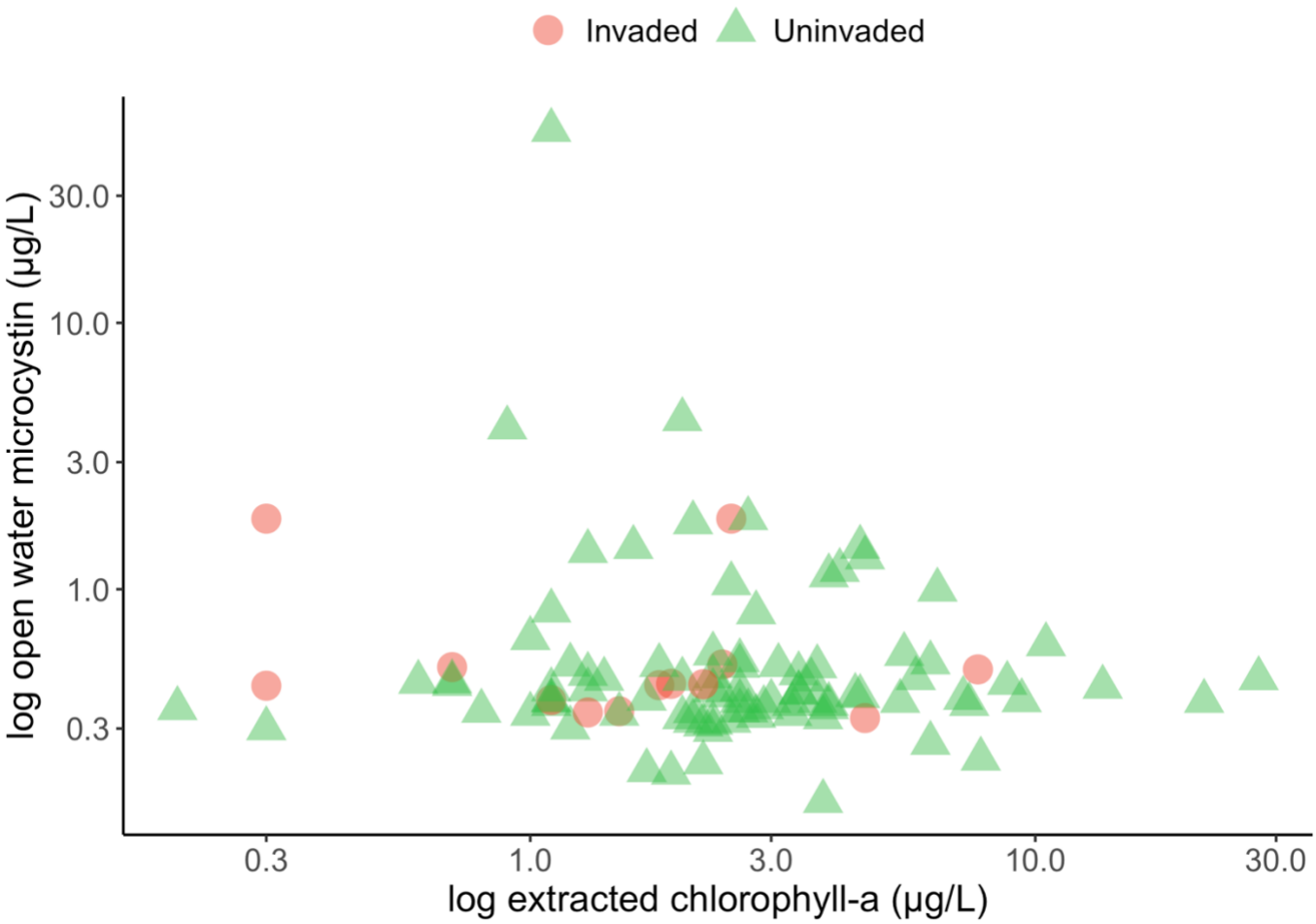


Fig 2-S2. Relationship between chlorophyll-a and open water microcystin. Red circles- invaded lakes; green triangles- uninvaded lakes. Chlorophyll-a was not a significant predictor for open water microcystin in both invaded and uninvaded lakes.

Appendix B: Supplementary tables and figures for Chapter Three

Table 3-S1. Lake descriptions (location, physical characteristics, invasion status). For trophic status: M= "mesotrophic," ME= "mesoeutrophic," MO= "mesoligotrophic."

Lake	Trophic Status (2018)	Mean Depth (m)	Catchment Area: Surface Area	Invasion Status	Year of Invasion	Quaggas present?
Honeoye	ME	5.0	14.0	Invaded	1998	No
Silver	ME	7.0	14.0	Invaded	2001	No
Owasco	M	29.0	19.0	Invaded	1997	Yes
Crooked	M	4.9	19.38	Uninvaded	NA	No
Song	M	4.0	5.80	Invaded	2017	No
Tully	M	4.7	0.74	Uninvaded	NA	No
Upper Little York	M	9.9	189.86	Invaded	2013	No
Cazenovia	M	7.1	4.65	Invaded	1997	No
Eaton Brook	MO	6.2	16.58	Invaded	1999	No
Craine	M	4.3	3.66	Invaded	2007	No

Table 3-S2. CSLAP trophic status guidelines

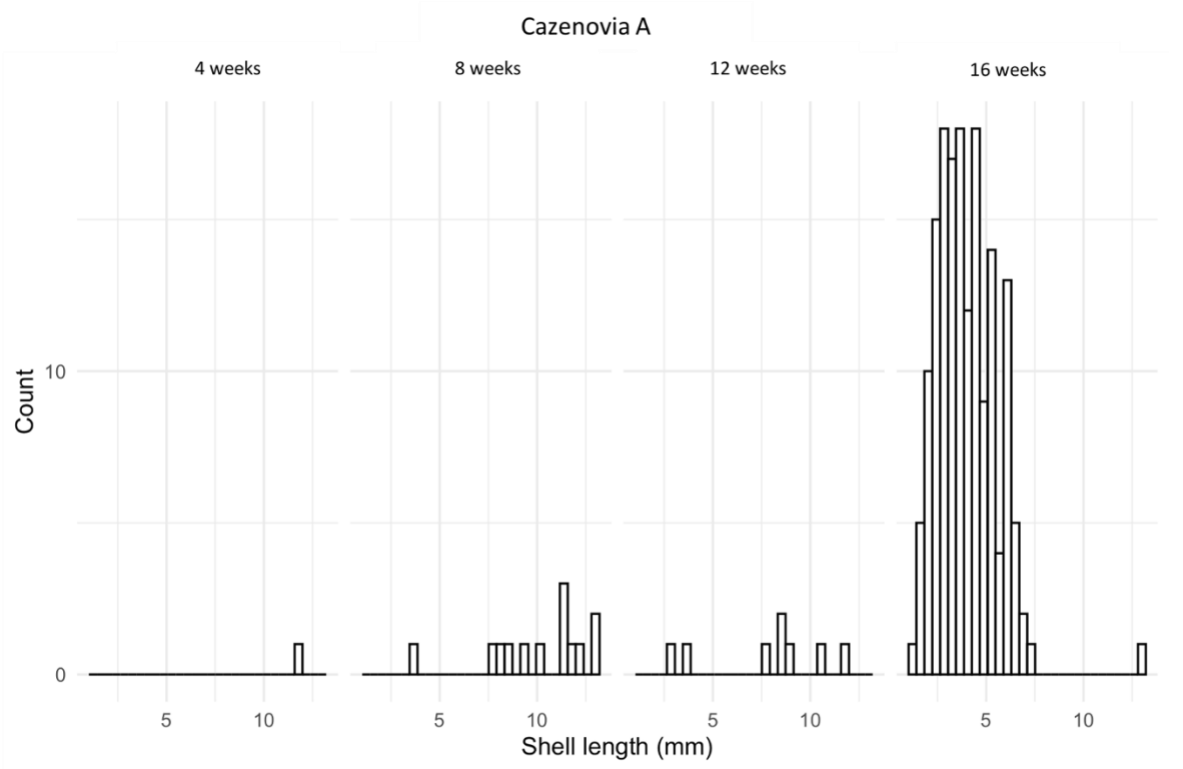
Parameter	Oligotrophic	Mesotrophic	Eutrophic
Transparency (m)	> 5	2–5	< 2
Total Phosphorus (µg/L)	< 10	10–20	> 20
Chlorophyll *a* (µg/L)	< 2	2–8	> 8

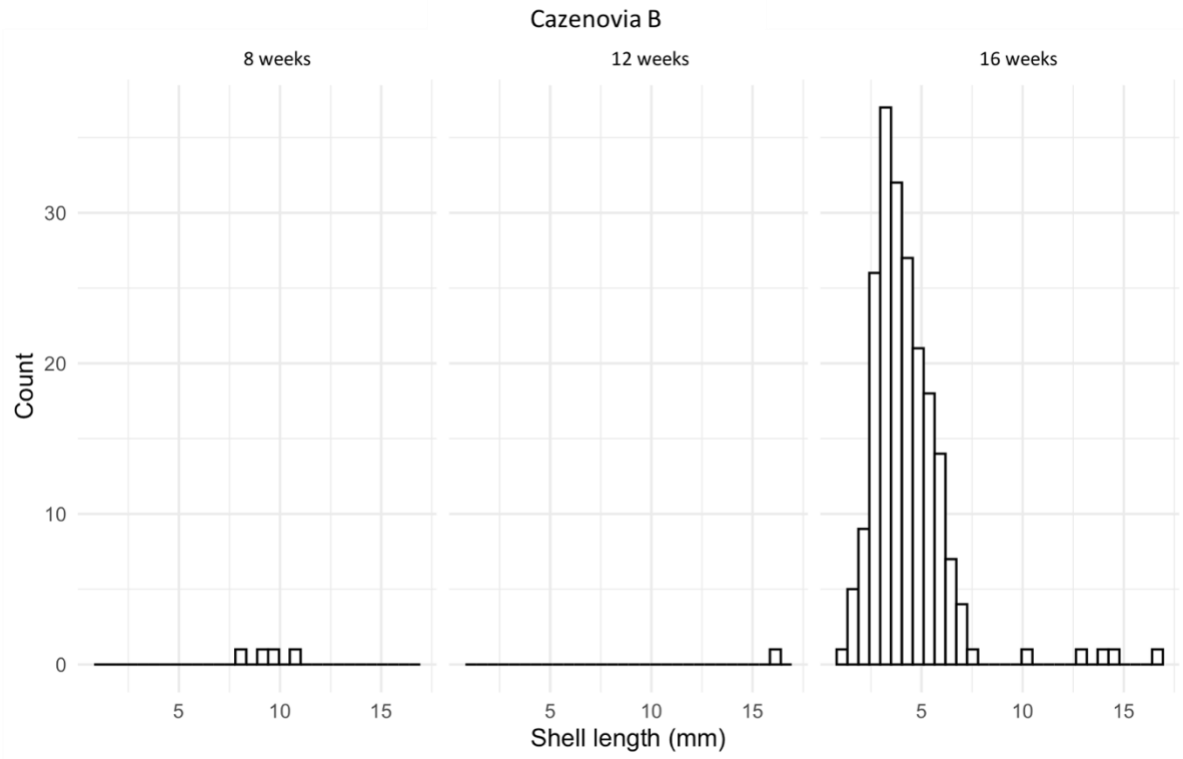
Table 3-S3. Model results for abundance as predicted by deployment time length and the number of years invaded. Model was a generalized linear mixed effects model with a negative binomial distribution and log link.

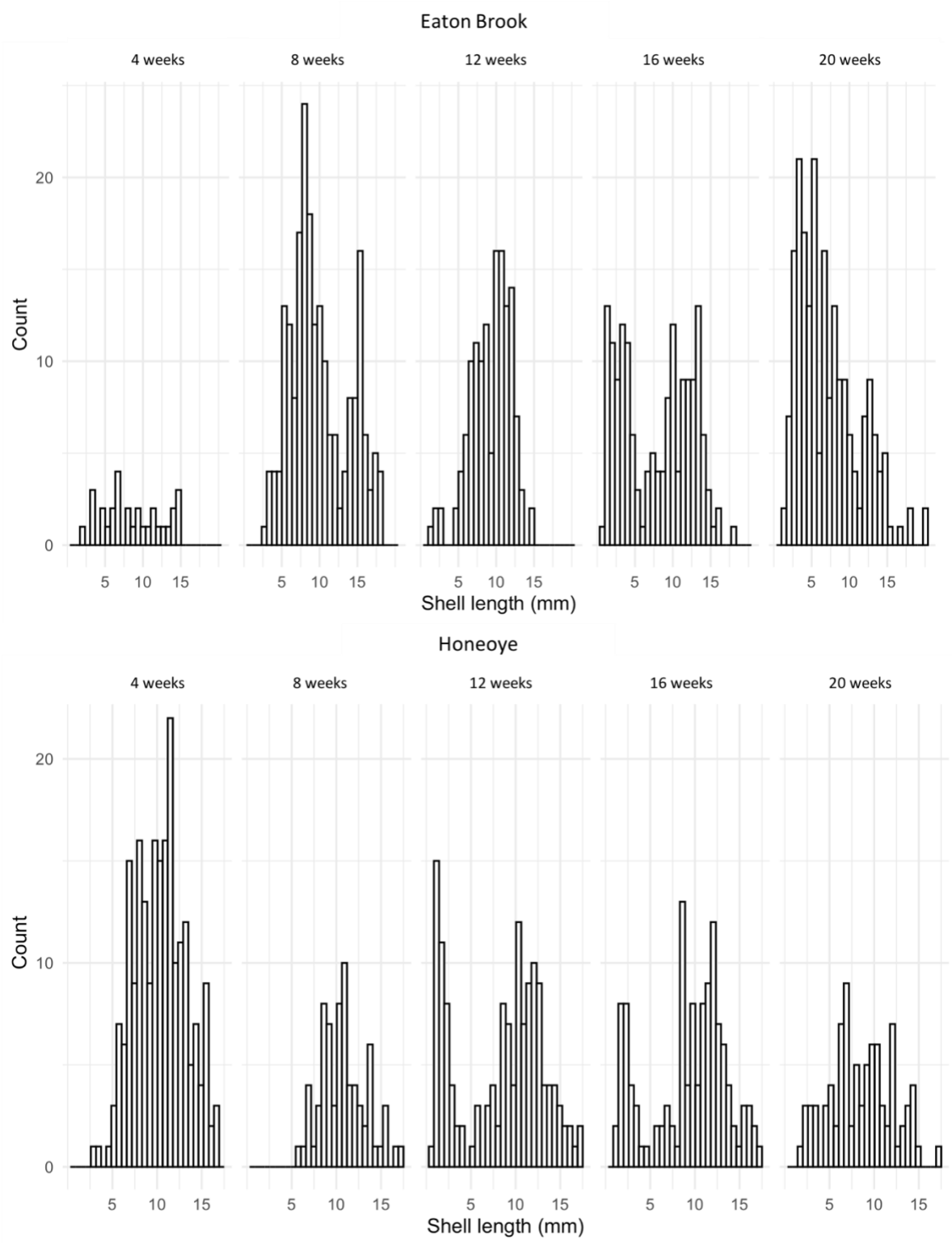
	Abundance (mussels/m$_2$)		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	611.18	203.37 – 1836.77	**<0.001**
Deployment Time Length (weeks)	1.05	1.00 – 1.11	**0.047**
Years Invaded	0.99	0.94 – 1.04	0.674
Random Effects			
σ_2	0.55		
$\tau_{00\ Lake}$	0.14		
ICC	0.20		
N $_{Lake}$	8		
Observations	35		
Marginal R_2 / Conditional R_2	0.143 / 0.318		

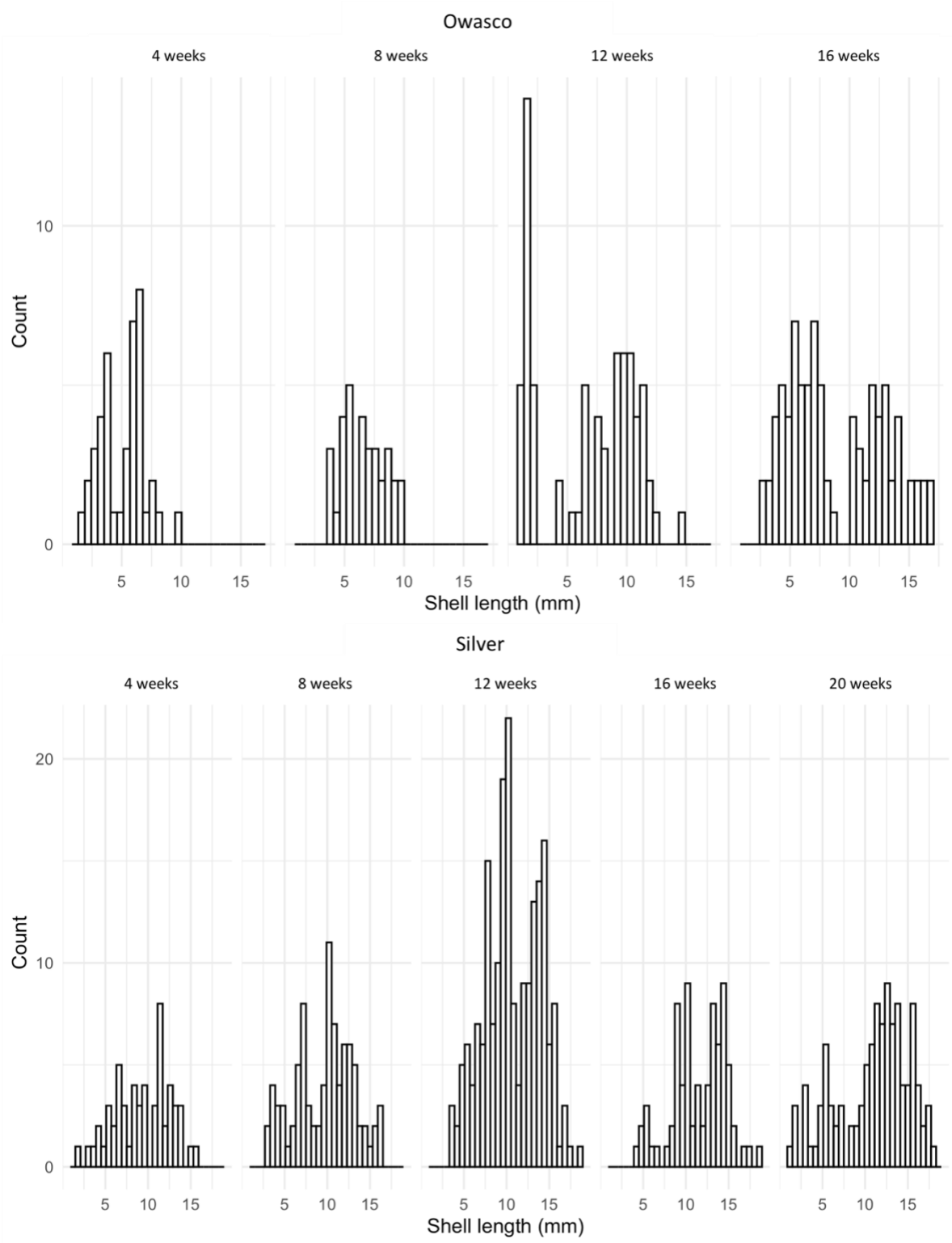
Table 3-S4. Model results for shell length as predicted by deployment time length. Model was a linear mixed effects model.

	Length (mm)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	7.83	6.12 – 9.54	**<0.001**
Deployment Time Length	0.01	-0.01 – 0.03	0.246
Random Effects			
σ_2	11.58		
$\tau_{00\ Lake}$	5.86		
ICC	0.34		
N Lake	8		
Observations	3518		
Marginal R_2 / Conditional R_2	0.000 / 0.336		


Cazenovia A
4 weeks
8 weeks
12 weeks
16 weeks
Count
0
10
5
10
Shell length (mm)


Cazenovia B
8 weeks
12 weeks
16 weeks
Count
0
10
20
30
5
10
15
Shell length (mm)


Eaton Brook
4 weeks
8 weeks
12 weeks
16 weeks
20 weeks
Count
0
10
20
5
10
15
Shell length (mm)
Honeoye
4 weeks
8 weeks
12 weeks
16 weeks
20 weeks
Count
0
10
20
5
10
15
Shell length (mm)


Owasco
4 weeks
8 weeks
12 weeks
16 weeks
Count
0
10
5
10
15
Shell length (mm)
Silver
4 weeks
8 weeks
12 weeks
16 weeks
20 weeks
Count
0
10
20
5
10
15
Shell length (mm)

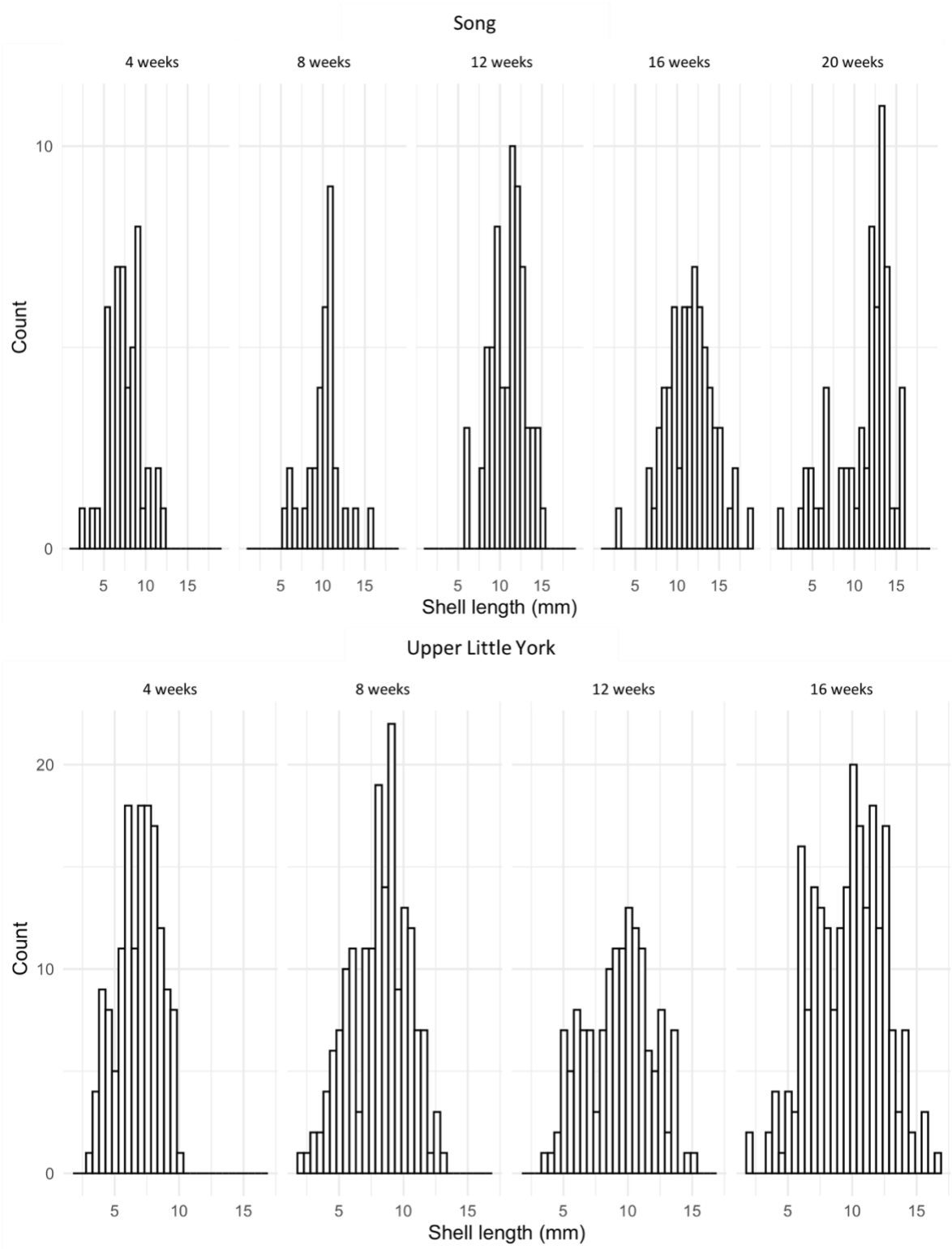


Figure S3-1. Shell length distributions by lake.

Curriculum Vita

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WORK EXPERIENCE

SUNY COLLEGE OF ENVIRONMENTAL SCIENCE AND FORESTRY, NEWCOMB NY
Instructional Support Specialist. Summer 2020

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Graduate Research Assistant. May 2018-May 2020

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A.S., Magna Cum Laude, Math and Science. August 2016

RELEVANT COURSEWORK

Coding and Statistics

- APM 510: Statistical Analysis
- APM 620: Analysis of Variance and Experimental Design
- APM 645: Non-parametric Statistics & Categorical Data Analysis
- EFB 796: Intro to R and Reproducible Research

Ecology

- BTC 498: Research Problems in Biotechnology
- EFB 496: Field Ornithology
- EFB 624/525: Limnology and Practicum
- EFB 681: Aquatic Ecosystem Restoration and Enhancement
- EFB 524: Freshwater Wetland Ecosystems

PUBLICATIONS

Field V., Gorney R., Mueller N., Schulz K, Razavi N.R. Using citizen-science data to evaluate the role of dreissenid mussels in harmful algal bloom formation in low-nutrient lakes in New York State, U.S.A. (In preparation)

PRESENTATIONS

Using Citizen Science to Inform the Role of Invasive Mussels on HABs in New York. Field V. New York State Federation of Lake Associations Annual Conference. Lake George, NY. May 4-5, 2019. Presentation